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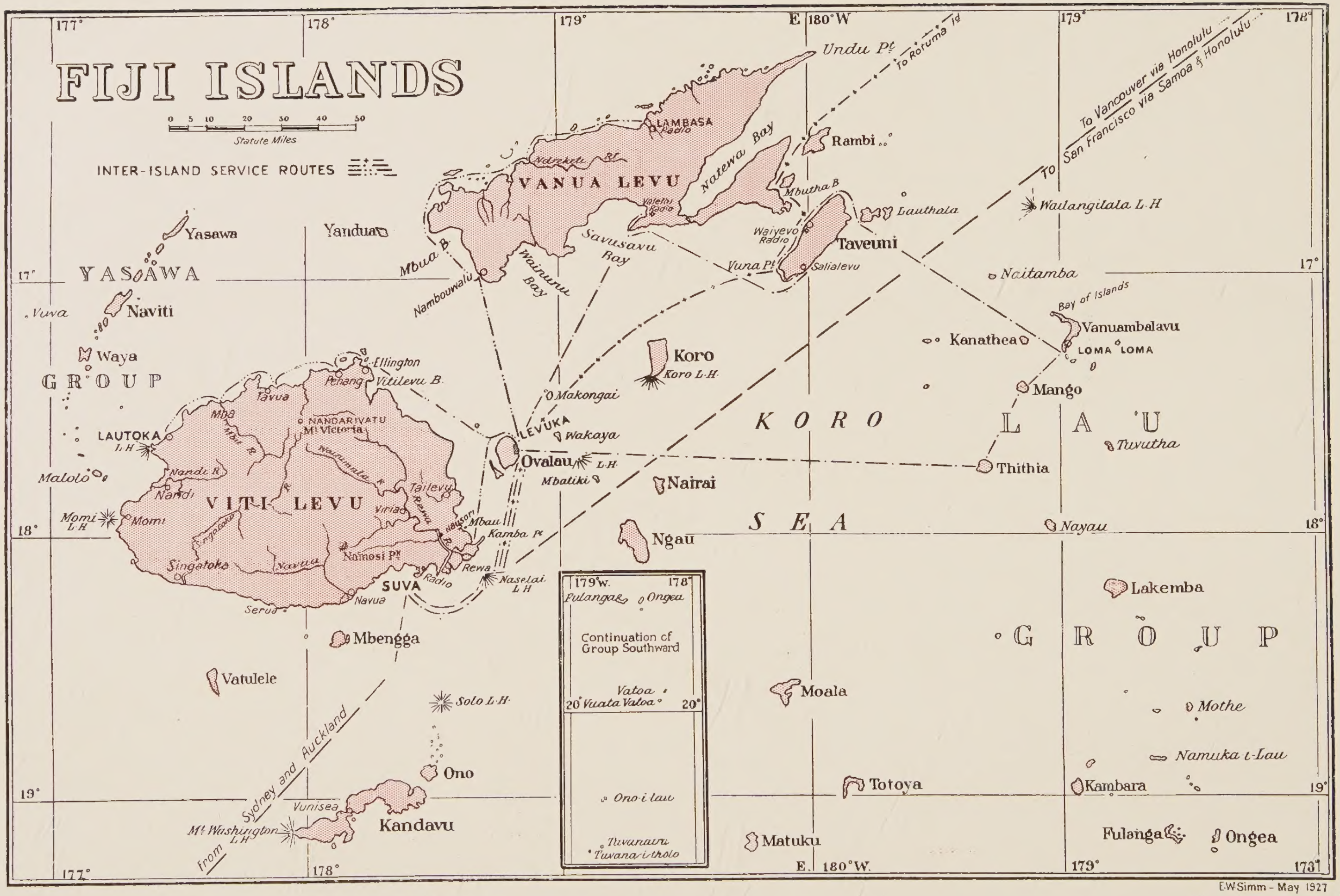
FIJI ISLANDS
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GROUP
Yasawa
Naviti
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Mba
Mba R
Tavua
Ellington
Penang
Vitilevu B.
NANDARIVATU
Mt Victoria
Wainimala R
VITI LEVU
Singatoka
Navua
Namosi Pt
Serua
Tailevu
Viria
Rewa R
Rewa
SUVA
Radio
Mbau
Kamba Pt
Naselai L.H
Mbengga
Vatulele
Solo L.H
Ono
Kandavu
Vunisea
Mt Washington L.H
from Sydney and Auckland
VANUA LEVU
LAMBASA Radio
Ndreketi R
Mbua B.
Nambouwalu
Wainunu Bay
Savusavu Bay
Valeni Radio
Natewa Bay
Undu Pt
To Rotuma Id
Rambi
Mbutha B
Waiyevo Radio
Vuna Pt
Taveuni
Salialevu
Lauthala
To Vancouver via Honolulu
To San Francisco via Samoa & Honolulu
Wailangilala L.H
Naitamba
Bay of Islands
Vanuambalavu
LOMA LOMA
Kanathea
Mango
Thithia
Tuvutha
LAU
KORO SEA
Koro
Koro L.H
Makongai
LEVUKA
Wakaya
Ovalau
L.H
Mbatiki
Nairai
Ngau
Nayau
Lakemba
GROUP
Moala
Mothe
Namuka-i-Lau
Kambara
Totoya
Matuku
Fulanga
Ongea
179°W.
178°
Fulanga
Ongea
Continuation of Group Southward
Vatoa
20°
Vuata Vatoa
20°
Ono-i-lau
Tuvanaira
Tuvana-i-tholo
E. 180°W.

E.W.Simm - May 1927

[*Frontispiece*

THE COCONUT MOTH IN FIJI

A HISTORY OF ITS CONTROL BY MEANS OF PARASITES

BY

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INTRODUCTION

In 1924 a Committee was set up by the Government of Fiji to deal with the problem of controlling the pretty little purple moth known as *Levuana iridescens*, B.B., which was destroying the leaves of coconuts and reducing the production of copra. This Committee was styled the Levuana Committee and had the then Acting Superintendent of Agriculture, Mr. A. Despeissis, as chairman, with the Senior Elected Member of Legislative Council, the Hon. Sir J. M. Hedstrom, and a prominent member of the planting community, Edward Duncan, Esq., as members. The two latter gentlemen were largely and directly interested in the copra or coconut industry of the Colony. At this time the *Levuana* problem had become so acute as to imperil the copra industry, and amongst other things a prize of five thousand pounds was offered to any one who could indicate a remedy.

In the same year, 1924, the Hon. Sir J. M. Hedstrom went to London in connection with the Wembley Exhibition, and was invited by the Government of Fiji to discuss the *Levuana* problem with the Home Authorities with a view to stimulating the campaign. He was advised by Dr. G. A. K. Marshall, C.M.G., the Director of the Imperial Bureau of Entomology, that the most likely way to find a solution would be to employ some entomologists for a few years to study the problem on the ground. His recommendations, communicated to the Government of Fiji, resulted in the appointment of the Senior Author as director of the Levuana Campaign and of Messrs. R. W. Paine and T. H. C. Taylor as assistants.

With these appointments, the offer of the prize was withdrawn and the work of the Levuana Committee, with Tothill newly constituted as chairman, was financed by an export tax of two and sixpence per ton of copra and an equal contribution from general revenue, making an annual budget of five thousand pounds per annum. Sir Maynard Hedstrom and Mr. E. Duncan have continued to act as unofficial members of the Levuana Committee, and by their untiring interest and support have contributed largely to the success of the campaign. The hard work and enthusiasm of Messrs. Taylor and Paine cannot be briefly described nor appreciated.

We are indebted to so many people for assistance in the prosecution of the campaign that it is impossible to mention all by name. Upon arrival in Fiji we were given every possible assistance by the then Acting Governor, the late Mr. T. E. Fell, C.M.G. ; and it is a pleasure to acknowledge the unfailing help and kindly advice of His Excellency the Governor, Sir Eyre Hutson, K.C.M.G., in whose term of office the control of this pest has been concluded. Our colleagues in other departments of the Civil Service have given assistance most freely, and we have had full co-operation with all members of the Agricultural Department, particularly with Mr. H. W. Simmonds, Government Entomologist, who spent some months in Java and the Malay States in the study and collection of parasites of *Artona*, a Zygaenid moth related to *Levuana*. The Director of the Imperial Bureau of Entomology, Dr. G. A. K. Marshall, has been keenly interested in the project and has given advice and assistance at many points. The scientific staffs at the Hawaiian Sugar Planters' Station, at Buitenzorg in Java and at Kuala Lumpur in the Federated Malay States have rendered aid that is gratefully acknowledged. In the difficult matter of transport material assistance was rendered by the Government Railways in the Federated Malay States and by Messrs. Cayzer, Irvine and Co., who altered the route of one of the Clan Line cargo steamers running from London to Suva so as to call for a shipment of parasites.

Authorship

Subject to slight exceptions, the Introduction, the Account of Previous Work, and the General Account of the Campaign instituted in January 1925 have been written by the Senior Author; the Account of the Levuana Moth, the systematic section, the section dealing with Relationships and Phylogeny and the section dealing with Origin and Natural Habitat have been written by Taylor; the short sections dealing with allied Zygaenids and their Natural Control, the Parasite Chalcid B, and with the Egg-parasite having the appalling name of *Trichogrammatoidea nana* have also been written by Taylor. The very considerable remainder of this report, chiefly on the detailed studies of *Levuana* and its control that have been made in Fiji, have been written by Paine.

As to the illustrations, the photographs used in the twenty-two uncoloured plates were taken, developed and printed by Paine; the paintings of various insects represented on Plates XXX to XXXIV inclusive were done by H. W. Simmonds; and the paintings used for Plates I to VII, depicting typical scenes in the *Levuana* area prior to the arrival of *Ptychomyia*, were done by W. J. Belcher. With insignificant exceptions, the text-figures were drawn by Paine and Taylor.

A STATEMENT OF THE PROBLEM IN JANUARY 1925

In January 1925 the Colony had barely emerged from the difficult post-war period. There had lately been a strike among the East Indian labourers employed in the Sugar Cane industry, and that industry, the premier one in the Colony, was undergoing a reorganisation. The export of bananas to Australia had come to an abrupt termination owing to adverse legislation. The Colony was carrying an overdraft on revenue account of almost £400,000, and the copra industry was threatened with disaster from the *Levuana* moth.

The copra industry occupies a somewhat unique position in the economic structure of the Colony, though the Blue Book tells us that it ranks second to cane sugar in money value. In the first place, it is a more permanent industry than sugar cane. Once the coconut is planted, it goes on growing for nearly a century, and after the first ten years or so produces a regular monthly crop of nuts that can be gathered in by three or four generations of mankind in succession. When low prices rule, no one ever thinks of cutting down coconut trees and planting the land to another crop because it is almost certain that prices will ascend before permanent injury has been done to the trees through neglect or even temporary abandonment. Since coconuts compete with ground nuts, and prices for the two oils show corresponding variations, the automatic shrinkage in the acreage sown to ground nuts when prices rule low soon brings the price of both oils to their normal value. Copra, which is a Hindustani name for the dried meat of the mature coconut, is about two-thirds oil. It is used chiefly for the production of soaps and of edible fats, commodities which are vital to Europe and America and likely to continue so for centuries. While it is sincerely to be hoped that the sugar industry of Fiji will prosper for centuries, it cannot be denied that it is a less stable industry than copra. On account of the large overhead expenditure, the sugar mills cannot well afford to be idle during periods of low prices. At the present time the Colony enjoys a substantial preference for its sugar in the British Empire, but the principle of the preference has not stood the test of many years, and it is possible that it will be abandoned if and when a political party comes into power at Home hostile to the principle. Sugar cane also has a serious competitor in the sugar beet, and there is a tendency toward an over-production of cane sugar that has had very serious consequences in recent years in Cuba. Another respect in which coconuts are more important to this Colony than cane is that from time immemorial the coconut palm has been a mainstay of the Fijian race. In times of failure of taro and yams the coconut has provided meat and in times of drought has provided drink for populous villages in outlying islands. In a degree the tree has been the dairy cow of the Native Race and has enabled healthy children to be raised without the aid of the domestic cow. Thus the coconut is the chief source of material wealth—of ready cash—of the Fijians, and it enables islands to be inhabited and prosperous that would otherwise be unpopulated and barren.

Finally, the wealth derived from coconut trees remains largely in the Colony, while part of that derived from sugar cane goes out of the Colony to shareholders of a Company that has headquarters in Sydney.

In January of 1925 the threat of disaster to the coconut industry had been hanging as a cloud for several years in spite of much that had been done to try to secure control of the *Levuana* moth. Banks and business houses were aware of the position, and the value of coconut estates had depreciated considerably.

The alarm was caused by *Levuana iridescens* breaking its traditional bounds on the large island of Viti Levu and finding its way to Ovalau and neighbouring islands. It had been present on Viti Levu for so many years that coconuts were there not regarded as a source of wealth, and the agriculture of this island had settled into other grooves. Ovalau and the neighbouring islands of Moturiki, Cagalai, Leleuvia and Naigani, however, depended almost wholly upon coconuts, and when, on account of the abundant food supply, the insect developed outbreaks and repeatedly defoliated the coconut trees on those islands, no nuts were produced and the revenue suddenly ceased. Even this, however, was not the gravest concern, as the islands mentioned produced but 500 tons of copra per annum in a Colony producing about 30,000 tons. The gravest feature was that as Levuka on Ovalau was the gateway to Vanua Levu, Taveuni and the Windward Islands where most of the copra is produced, it was felt to be certain that unless the insect could be checked, it would, in the course of time, further break its bounds and ruin the whole industry.

Some idea of the extent of injury by the insect will be obtained by glancing at the illustrations in this report, and a detailed account thereof will be found later. The visible effects were so striking, however, that an account of the position in January 1925 is not complete without a brief comment. Outbreaks of insects that defoliate trees have something in common, whether it be the Nun moth in Europe, the Gypsy moth in Massachusetts, the Forest tent moth or the Spruce Bud worm in Eastern Canada, or the Levuana moth in Fiji. In all cases there are countless millions of the insects present and the verdure of the trees attacked is replaced by another colour. A poplar forest devastated by tent caterpillars becomes a twig-coloured desolation, the spruce and fir forest defoliated by bud worm turns a rusty hue and gives the appearance of having been scorched for mile upon mile with living flame, while the coconuts on the islands under attack by *Levuana* turned from the normal fringe of shining, waving green fronds to a border of lifeless grey. Ovalau is roughly thirty-five miles in circumference, and every mile of shore-line has its quota of coconut palms. At the close of an outbreak not a single green coconut palm was to be seen, even single trees upon the slopes standing out as grey objects plainly marked from the surrounding greens of forest trees and grass. At the end of each outbreak most of the insects would die from starvation, but a few would be left, as will be explained later, on what we have called " carry over " trees. The central unfolding leaf on each tree would not be attacked to an appreciable extent, and when the insects had been depleted by wholesale starvation, a crown of green leaves would develop above the grey ones. The improved appearance would encourage the community to believe that the scourge had passed and that all would be well in the course of time. As soon, however, as a sufficient food supply was available, a new outbreak would develop from the " carry over " trees, and in a few months the entire fringe would once more be desolate and grey. By January of 1925 there had been a sufficient number of outbreaks to show that the insect was unlikely to die out of itself, the trees had ceased to bear, and it seemed that coconuts could not be grown commercially in the presence of *Levuana*.

HISTORICAL

AN ACCOUNT OF PREVIOUS WORK

The first definite record of the occurrence of this insect is by J. Horne, who visited the Colony at the invitation of Sir Arthur Gordon in 1877. He says (*Year in Fiji*, p. 174):

> "Excepting Viti Levu, the coconut thrives remarkably well in all parts of Fiji and the trees are generally as healthy and fruitful as in the best plantations I have seen in the Seychelles or Ceylon. In Viti Levu the leaves of the trees are attacked by a caterpillar to such an extent as to injure the health of the tree and prevent it bearing fruit abundantly."

Previous to this there is a doubtful record by the very observant botanist, Berthold Seemann, who visited the Colony in 1860. He says (*Flora Vitiensis*, p. 278. London, 1869):

> "It is to be regretted that so few plantations of coconut palms are formed by white Settlers. . . . Every part of the smaller islands and the sea borders of the larger are localities suitable for this purpose. Only Bau, Viwa and the districts adjacent form an exception, the trees as soon as they have reached a certain height become diseased; their leaves look as if dipped in boiling water . . . a thick layer of marl forming the subsoil of those districts seeming to oppose that ready drainage which the coconut tree requires." *

In the still earlier writings of various Missionaries we have been able to discover no reference to a coconut disease on Viti Levu. Neither does the study of tree trunks afford any conclusive evidence. Each defoliation of a tree by *Levuana* leaves a constriction in the growing part of the trunk, and as a normal tree produces a new leaf each month, one can theoretically tell the approximate age of the lowest or oldest trunk constriction on any given tree. Practically the matter is complicated by the fact that all constrictions are not due to *Levuana* and by the fact that in the lower part of an ancient tree the leaf scars are so weathered as to make an accurate tally impossible. The evidence from trunk constrictions is not sufficiently definite to enable us to say that *Levuana* was present in Fiji in 1860, but indicates a wide distribution of *Levuana* on Viti Levu at and a few years prior to 1877. In the last twenty years the evidence from trunk constrictions shows that on the windward side of Viti Levu outbreak has succeeded outbreak in rapid succession, and that on the leeward side the intervals between outbreaks have been longer.

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* This remark of Seemann's has been interpreted by Knowles, Simmonds and others as a possible, or even probable, indication of the presence of *Levuana* in 1860. Since it is a fact that bad drainage and impervious subsoils cause a yellowish and unhealthy condition in coconut leaves, we see no justification in departing from Seemann's own explanation.

Before speaking of the plans made in January 1925 to deal with this situation, it is convenient at this point to give an account of steps that had already been taken or that were in progress to remedy conditions.

(*a*) **Mechanical Control.**—When the first outbreak occurred on the little coral island of Cagalai, an attempt was made by the Government to prevent the insect spreading across the three-mile strip of water to Moturiki by cutting down the ten acres or so of coconut palms upon this little island. The measure was not successful, probably because extensive moth flights had already occurred, and from what we now know it is more than likely that several separate little outbreaks were developing on Moturiki at the time the action was taken. Once the insect was established on Moturiki, attempts at mechanical control had to be abandoned as the outbreak rapidly assumed proportions beyond any hope of checking it by this method.

When the outbreak reached the old capital of Levuka, steps were taken to minimise the danger of moths swarming upon cutters and other craft and so being carried to the main coconut areas of the Colony. In the first place, all coconut trees within half a mile of the wharf were cut down. This precautionary measure did undoubtedly minimise the danger but came as a hard blow to the citizens of the beautiful little town of Levuka, one of the chief glories of which consisted of the numerous coconut trees.

(*b*) **Inspection of Inter-Island Shipping.**—Another step taken was to make regulations under which all vessels clearing from an infested for an uninfested part of the Colony were required to report for inspection at one of three ports, namely, Suva, Levuka or Lautoka.

(*c*) **Biological Control.**—Two curious facts in connection with *Levuana* had led to explorations being made in various countries for the purpose of discovering, if possible, an ancient home of this insect in which natural enemies might be discovered. In the first place, the insect had a remarkable distribution, and secondly, it had no parasites of any consequence.

The distribution, in so far as known, was not only confined to the Colony of Fiji but for many years was narrowed down to the single island of Viti Levu in that Colony together with a few small islands close to its coast (see Frontispiece). Such a distribution did not prove *Levuana* to be an introduction into Fiji, because there are a few other living organisms known to have an equally restricted distribution, such as an orchid confined to the neighbourhood of a small lake on Taveuni and a *Pritchardia* palm confined to the remote island of Fulaga in the Windward Group. Most, however, of the animals and plants native to Fiji are distributed somewhat widely throughout suitable parts of the Colony, and it was possible that the narrow distribution of *L. iridescens* was due to its being a comparatively recent arrival in the Colony.

The absence of parasites was equally strange for a native insect, and other species of ZYGAENIDAE in Malaya, Java, New Guinea, and the Solomon Islands are all preyed upon effectively by parasitic insects.

This interesting and enigmatic question of the origin of *Levuana* is discussed in detail later on (see p. 56), but enough has been said here to indicate that on the evidence available, there was a possibility, or even probability, of finding *Levuana iridescens* in a condition of biological control in some place other than Fiji.

(*d*) **Search for Levuana in Melanesia.**—For the purpose of searching for *Levuana*, therefore, the then Acting Government Entomologist, Mr. H. W. Simmonds, was sent in June 1923 on an eight months' mission to the New Hebrides, Bismarcks, Solomon Islands, and northwest New Guinea. On the way he also visited Lord Howe Island and Norfolk Island. As a result he reports (Simmonds, 1924), " nowhere did I find anything to suggest the presence of *Levuana iridescens* or of any allied species."

(*e*) **A Mission to Queensland, Thursday Island, Java, Malaya and Borneo.**—In 1924 Mr. A. M. Lea, Government Entomologist of South Australia, was also employed by the Levuana Committee, for a year in the first instance, to carry the search farther afield. He was also asked to study the closely allied moth, *Artona catoxantha*, in Malay and Java and to endeavour to effect the introduction to Fiji of parasites known to occur upon that insect. Mr. Lea was accompanied by Mr. T. C. McNamara, a Plantation Inspector attached to the Fiji Service. One result of this expedition was the discovery of the larvae of a somewhat related insect called *Procris subdolosus* on Magnetic Island opposite Townsville in Queensland. A Tachinid fly parasite was bred from these larvae, but limitation of material prevented rearing parasites in quantity, and Mr. Lea did not attempt to bring them to Fiji. In the Malay States, Borneo and Java the mission was confined to looking for outbreaks of *Artona* in the right stage of development for making parasite collections. Messrs. G. H. Corbett, B. A. R. Gater and S. Leefmans, entomologists who had all studied the insect for a number of years, assisted Mr. Lea, and he succeeded in finding the material he required in Java.

Several species of parasites of *Artona* were collected in large numbers, and an attempt was made to bring them to Fiji in cold storage. The journey was long, the parasites began emerging near the beginning of it, many of them died before trans-shipment in Sydney, and only one or two forlorn adults, unequal to perpetuating themselves, survived on arrival in Fiji. Two such shipments were attempted, one accompanied by Mr. Lea, the other by Mr. McNamara.

The net result of the efforts toward effecting a biological control for *Levuana* prior to January 1925 was therefore disappointing. Although most of the main island groups between Fiji and Singapore, and also the Queensland coast, had been examined, *Levuana* had not been found, and no allied insect nearer than *Artona* had been discovered. The *Procris* already referred to as discovered by these missions is not as closely related to *Levuana* as is *Artona*. Moreover, the two abortive attempts to introduce the parasites of *Artona* had served to show how difficult it was to transport these insects alive in the tropics on a sea voyage four thousand miles in length and occupying nearly a month in time.

THE CAMPAIGN INSTITUTED IN JANUARY 1925

In January 1925 the position was not one that could be described as reassuring. A *Levuana* outbreak was in full progress on Ovalau, and the entomological missions referred to above had not succeeded in finding any other home of *Levuana* nor in finding any really close relatives of *Levuana* not already known. As our appointments were for two years only, it was necessary to adopt a plan of campaign immediately and to put it into execution promptly.

The Director had been fortunate, first in being granted the opportunity of discussing tentative plans with Dr. G. A. K. Marshall, C.M.G., in London, before proceeding to Fiji, and, second, in being allowed to interview a number of young men there as possible assistants, and to choose the two who have so well justified their selection.

On arrival in Fiji he placed the tentative plans drawn up in Ottawa and London before the Levuana Committee. On account of the limited time at our disposal it seemed wise to pursue a number of lines of effort simultaneously and to examine the minor as well as the major possibilities of help. Early in 1925 the Committee decided upon the following projects :—

A. Introduction of certain parasites from Hawaii.

B. To recommend to the Government that legislation be amended so as to improve the regulations for inspecting various craft proceeding from infected to non-infected islands in the Colony.

C. To experiment with poison sprays.

D. To experiment with the ant, *Oecophylla smaragdina*, known to destroy some insect pests.

E. To experiment with birds known to haunt coconut palms in Ceylon, India, or elsewhere.

F. To continue the search for *Levuana* and for closely related insects in places not already searched.

G. To re-attempt the introduction of the more important parasites of *Artona catoxantha*.

The work that followed each of these decisions may now be discussed in detail, and it will be convenient to do so in the above order, leaving what proved to be the most important to the end.

A.—Introduction of Certain Parasites from Hawaii

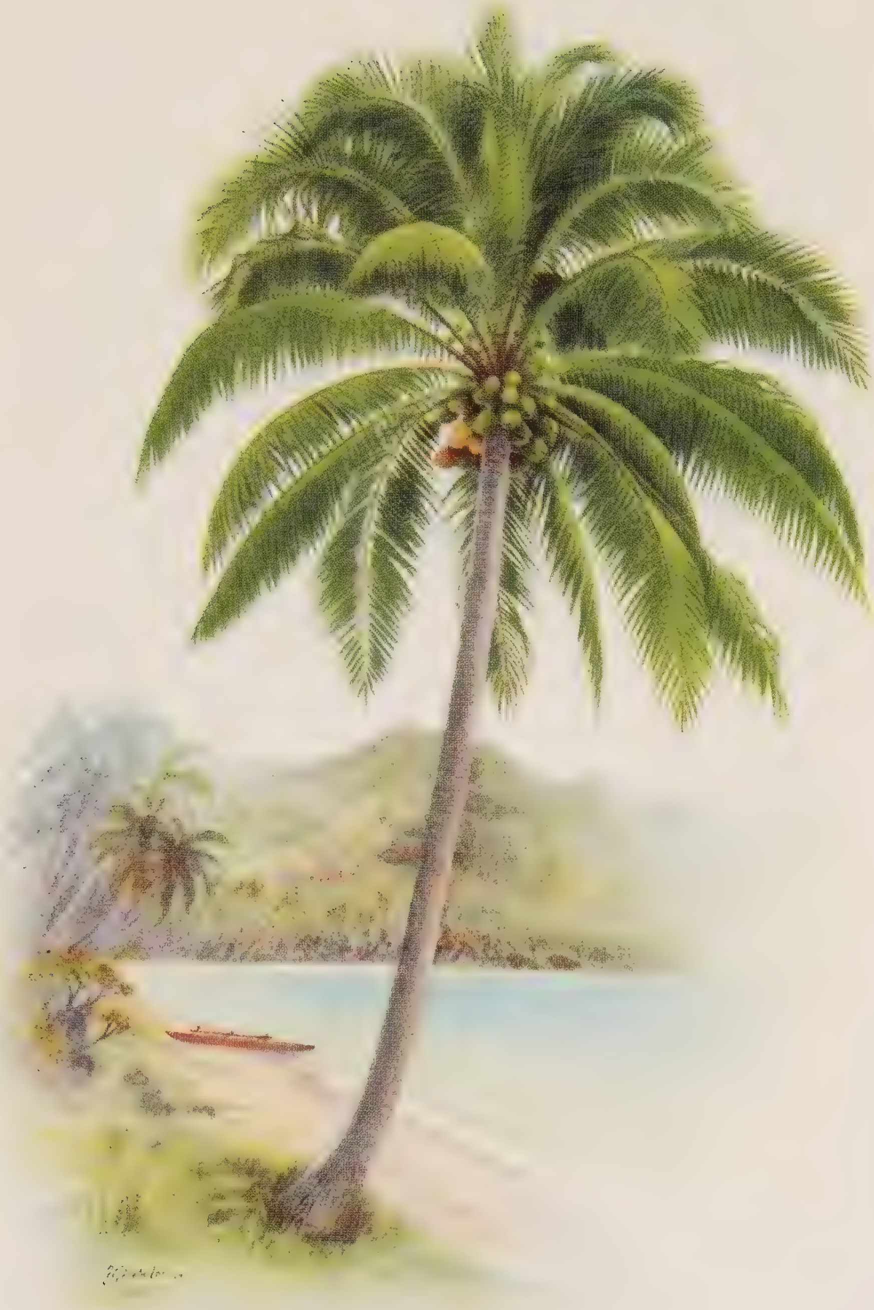
When the Senior Author passed through Hawaii en route for Fiji in December 1924, he made tentative arrangements, through the kindness of Officials at the Hawaiian Sugar Planters' Experimental Station and at the

PLATE I

A HEALTHY COCONUT PALM

A normal coconut palm in Fiji growing outside the *Levuana* area. The absence of trunk constrictions would in itself constitute ample proof that the tree had never been attacked by *Levuana*.

PLATE I



Station of the Federal Board of Agriculture and Forestry, for Messrs. Paine and Taylor to stop off for a month between boats and assemble a collection of parasites for shipment to Fiji. These arrangements were subsequently confirmed by the Committee, and the plan was carried out. The parasites in question were all generalised ones in the sense that they were known to attack a wide variety of hosts, and it was thought that one or two of them might be useful against *Levuana*. The fact was also appreciated that a month spent at laboratories so well staffed and equipped for biological control work as are those in Honolulu would be of value in familiarising us with the particular methods of transporting parasites that had been used so successfully by entomologists attached to the Honolulu Stations.

Particulars of the parasites introduced are as follows :—

Trichogramma pretiosa—an egg parasite.

About 100 specimens of this widely distributed parasite were liberated at Suva.

Macrodyctium omiodivorum.

About 100 specimens of this Braconid parasite attacking larvae were liberated at Suva.

Chalcis obscurata—a parasite of pupae.

About 100 specimens liberated at Suva.

Echthromorpha maculipennis.—Attacks pupae and prepupae that are not exposed.

About 12 adults liberated at Suva.

Frontina archippivora.—A Tachinid parasite attacking larvae of many Lepidoptera.

About 280 liberated at Suva.

Casinaria infesta.—Attacks larvae.

Less than 24 liberated at Suva.

Chelonus blackburni.—Attacks eggs of *Omiodes blackburni.*

About 12 specimens liberated ; prior to liberation these attacked *Levuana* vigorously in the insectary.

Euplectrus platyhypenae.

About 1,000 of these army worm parasites obtained from Mr. O. H. Swezey at the request of the Colonial Sugar Refining Company.

Three months later Tothill recovered specimens in force attacking Noctuid larvae at a point on the Princes Road about 8 miles from the point of liberation.

Only the last species is known to have become established, and none has proved to be of any value in the Levuana Campaign.

B.—Legislation to Regulate the Movement of Shipping from Infected to Uninfected Areas

In 1924 various regulations were made under the Diseases of Plants Ordinance of 1913 with a view to minimising the danger of *Levuana* spreading to new ground. All vessels proceeding from infested to uninfested territory were required first to report for inspection to either Suva, Levuka, or Lautoka. The port of Levuka was closed to shipping from October 27th to November 12th, 1924, during the destruction of all coconut trees within half a mile of the wharf.

In 1925 it was feared that evasions of inspection were occurring, and through the co-operation of Planters and others living on the important islands of Vanua Levu and Taveuni, a second inspection was arranged for on those two islands. Certain points of entry were gazetted and a voluntary inspector appointed for each point. All vessels arriving were required to put in for inspection at one of these places and obtain a certificate from the Inspector. This had the immediate effect of tightening up the vessel inspection system generally, particularly at a time when *Levuana* was rampant on Ovalau.

With minor modifications made for the purpose of removing some of the more conspicuous hardships caused particularly to cutter owners, this double system of inspection remained in force until the beginning of 1928, by which time the *Levuana* moth had been reduced to a condition of impotency. We take this opportunity of expressing appreciation to all those voluntary inspectors who for nearly three years co-operated so willingly to make this inspection effective. A word of appreciation is also due to the owners of vessels who put up with the daily inconvenience caused by these regulations and who for the most part suffered in silence and co-operated fully.

C.—Spraying Experiments

Both Mr. F. P. Jepson and Mr. C. H. Knowles had found that larvae of *Levuana* could be killed by spraying the leaves with arsenate of lead at a strength of 30 ounces to 25 imperial gallons of water, but as there was no machine available for applying the spray to tall trees the experiments had been discontinued.

Reports of new outbreaks were frequent in the early part of 1925, and the Committee was kept busy investigating them. There was a definite risk of the insect spreading to Vanua Levu or Taveuni before any biological check could be secured, and in view of this risk, it was decided to pursue the spraying experiments further, in order to have a mechanical remedy at hand for dealing with new outbreaks should they occur.

A series of tests was made in 1925 with a hand-spraying device on some small coconut palms in Government House Grounds. It was necessary only to consider stomach poisons, and of these, three were tried, namely, Paris green, calcium arsenate, and lead arsenate. Four strengths were tried, in each case ranging from what might be termed a weak to a strong mixture.

Paris green was first tried without lime to see whether leaf injury would occur despite the firm texture of the coconut leaf. The free soluble arsenic always present in this product caused a large amount of so-called burning, and the experiment proved that Paris green should not be used on coconut leaves without lime. Adhesion to the leaf surface was poor, and the use of this material was found, therefore, to be unsatisfactory.

In the case of calcium arsenate, the killing power was satisfactory at a strength of 2½ lbs. to 40 imperial gallons. Adhesion was also good, and the material remained on the leaves for twelve months.

The best material of the three was lead arsenate, at a strength of 5 lbs. of paste (=2½ lbs. dry) to 40 imperial gallons. The results were deemed sufficiently good to warrant the purchase of a power spraying machine.

An important point in the experiments was that sea water was used instead of fresh water because this latter commodity is frequently difficult to obtain near coconut plantations, while sea water is generally available. Many plants are injured or killed if sprayed with sea water, but the coconut being essentially a maritime plant is able to withstand a good deal of salt water even on the foliage, and in the experiments no foliage injury whatever was noted as a result of using sea water instead of fresh water.

Coconut palms are taller than most trees customarily sprayed, some of them reaching a height of 80 feet or more, and it was necessary, therefore, to use a machine sufficiently powerful to deliver a solid stream type of spray from the ground to the top of the trees met with in an average plantation. A FitzHenry Guptill Standard A.A. Model was purchased and mounted for trial on a decked punt. A galvanised iron shelter was built over the plant to protect it from rain and sun and to afford accommodation for the labour and the boat crew. A launch for towing this punt was made available by the Public Works Department.

At the end of a period of three months devoted to trials, it was found that the machine would be a valuable aid in dealing with initial outbreaks of *Levuana* on Vanua Levu or Taveuni, and after ordering an extra ton of lead arsenate to be on hand in case of an emergency the machine was taken in charge for safe keeping by the Public Works Department. Fortunately the emergency never arose, and the capacity of the machine to deal with an actual outbreak has not been tested. The main results of the trials referred to above are given in Council Paper No. 18 of 1926, and it seems unnecessary to reprint them here.

Toward the end of the trials, interest in spraying began to wane because the parasite *Ptychomyia* had begun to show promise of rendering the control of outbreaks by mechanical means unnecessary.

It may be mentioned for the information of those who may wish to spray coconut trees for other pests elsewhere that, on days when trade winds were not blowing too strongly, there was no difficulty in spraying trees up to 65 feet, but that very calm weather was required for spraying taller trees.

The cost per tree worked out at between 2*d.* and 2½*d.*, but this could be reduced materially in plantations suited to the use of a motor truck. Costs were arrived at in the following way :—

Spraying Costs—Plan A

Estimating season's work at 100,000 trees.
,, value of plant at £1,000.
,, repairs and replacements at £50.
,, labour for an 8½-hour day of actual work, 9 hose boys at 3*s*., 1 engineer at 6*s*.
,, benzine at 21*s*. a case.
,, cost of towing for season at £100.
,, idle days for wind and rain at 50 per cent. of time.
,, life of plant at 5 years with depreciation of £200 annually.
,, lead arsenate paste at landed cost of £55 per short ton or 6½*d*. per lb.

	Block 1, 400 trees.	Block 2, 1,150 trees.	Block 3, 220 trees.	Block 4, 230 trees.	Block 5, 800 trees.
Actual spraying time	1 hour	1¾ hour	20 min.	½ hour	3 hours
Benzine	⅛ tin £0 1 4	½ tin £0 5 4	⅛ tin £0 1 4	⅛ tin £0 1 4	1 tin £0 10 6
Labour	0 3 10	0 6 8	0 1 4	0 1 11	0 11 6
Arsenical 30 lb. to a tank (400 gals.) .	0 19 6	1 19 0	0 9 9	0 9 9	2 8 9
Towing at 0·24*d*. per tree	0 8 0	1 3 0	0 4 5	0 4 7	0 16 0
Idle days	0 3 10	0 6 8	0 1 4	0 1 11	0 11 6
Interest on plant at 0·12*d*. per tree .	0 4 0	0 11 6	0 2 2	0 2 3	0 8 0
Depreciation at 0·48*d*. per tree . . .	0 16 0	2 6 0	0 8 10	0 9 2	1 12 0
Repairs at 0·12*d*. per tree	0 4 0	0 11 6	0 2 2	0 2 3	0 8 0
Total cost .	£3 0 6	£7 9 8	£1 11 4	£1 13 2	£7 6 3
Cost per tree . . .	1·8*d*.	1·6*d*.	1·7*d*.	1·7*d*.	2·2*d*.

Adhesion of the spray, particularly of lead arsenate, was practically perfect for a year—April 15th, 1925, to the same date in 1926—in the initial hand-spraying experiments. In the experiments with the power sprayer it was found that once the spray had properly hit a leaf and dried on it the material would remain on the leaf for two years—or, in other words, long enough to protect it for its useful life against *Levuana*. It should be understood, however, that this applies only to the under surface of the leaf where the larvae feed, which surface is for practical purposes protected against the driving and eroding force of ordinary rains. The trees sprayed in the two sets of experiments were subjected to the usual torrential rains that occur from time to time throughout the year but particularly between December and April. The rainfall at Suva for 1926 was 103·39 inches, and twice during the year 5·17 inches fell within 24 hours.

D. THE ANT, OECOPHYLLA SMARAGDINA

An ant called the Green Tree Ant (*Oecophylla smaragdina*) occurs in practically all the tropical lands lying between the Solomon Islands and Southern China. It is very conspicuous for the reason that it lives in various trees, including the coconut, in a conspicuous nest, sometimes a foot in diameter and composed for the most part of leaves woven together with a white, silk-like material. The habits of this ant have attracted a good deal of attention. Observations by Ridley (1890), confirmed by those of Doflein (1905) and of Dodd (1906), state that the nest is built in this remarkable way: The edges of two leaves are first pulled together by a series of workers bridging the gap between the two. When the gap has been adjusted to the proper size another series of workers come up, each carrying an ant larva between its front legs. By squeezing the larva gently with the mandibles, it is made to discharge a fine thread of silk, and by moving the larva slowly from edge to edge of the two leaves, a silken web is finally constructed that holds the leaves in place. The ant has an unpleasant bite that makes it well but unfavourably known, to natives at least, throughout its range. It is carnivorous and particularly insectivorous in habits, and it is known to keep down a number of insect pests within its range.

The Levuana Committee was not particularly anxious to introduce this ant into Fiji on account of its bite. However, the bite is not nearly as painful as that of the so-called Buli ant in Fiji, and it was decided to find out as an initial step whether the ant would feed upon *Levuana* larvae. Accordingly a queenless nest of living ants was obtained from Queensland. The ants arrived in apparently good condition and were offered *Levuana* larvae. In spite of being half starved as a result of the long journey, however, they evinced very little interest, and as this showed that the ant would be of little practical value in the biological control of that insect, it was decided not to introduce the species.

It has recently been shown by Paine and Tothill (a Reconnaissance Survey of Agricultural Conditions in the Solomon Islands Protectorate, 1929) that this ant is the principal factor in the biological control of the Coconut flower bug, *Axiagastus campbelli*, and in the event of that injurious insect finding its way to this Colony there is no question that it would then be desirable to introduce the Green Tree Ant.

E.—The Introduction of Insectivorous Birds from Ceylon and India

Pursuing the policy of exploring every possible avenue that might lead to the control of *Levuana* the Committee, on the advice of Tothill, decided to introduce and experiment with insectivorous birds that might possibly be of value. It was known in general that larvae of insects in the Zygaenid family are possessed of repugnatorial glands that make them distasteful to most insectivorous birds. Proof, however, was lacking for *L. iridescens*, and, as deductive evidence is frequently of little value in the field of applied biology, it was decided to put the matter to the test. The Committee was also aware that in the event of any birds introduced failing to be useful in controlling the moth it was probable that they would be useful in the control of other insects injurious to coconuts, such as the Coconut Walking Stick or Phasmid, the Brown Moth (*Agonoxena argaula*), the Leaf-Mining Beetle (*Promecotheca reichei*), and the Fijian Lesser Spathe Moth (*Tirathaba trichogramma*).

After considering birds in a number of countries, it was finally decided, on the advice of competent ornithologists, to experiment with birds from Ceylon and India. Arrangements were accordingly made for Mr. J. E. Ward, of Sydney, who has had considerable experience in travelling with insectivorous and other birds, to visit Ceylon and India and to bring to Fiji a consignment of White Vented Drongos, Magpie Robins, and three other species, if obtainable. Mr. Ward was unable to obtain three of the species on the list, but returned in due course with a good collection of Toddy birds and the two species mentioned above. These were placed in a special aviary constructed for them as an addition to the aviary maintained by a local bird enthusiast, Mr. A. H. Martin.

A series of experiments demonstrated that none of the birds would eat *Levuana* and that the Toddy bird was of little value for any other purpose. It was found, however, that the other two birds fed readily upon all stages of walking-stick insects or Phasmids, the Brown Coconut Moth and the Lesser Spathe Borer; and, in addition, that the Drongo attacked vigorously the introduced yellow hornet which has useful predacious habits but which has become so abundant as to be a source of such constant worry to pedestrians and riders in the country that it is desirable to reduce its numbers.

In view of these things the Director and the Committee were strongly in favour of liberating the Robins and Drongos on one of the more remote islands in the Colony where their progress could be watched from time to time. If they escaped from this island, it was clear that they would not affect the *Levuana* position as they did not feed upon this insect.

At about this time the following telegram was received :—

> "Director of Imperial Bureau of Entomology understands proposal to introduce insectivorous birds Islands of Fiji in connection with Levuana Campaign is now under consideration. Although extremely anxious in regard to any such scheme, he had thought at one time that introduction of birds which naturally eat larvae of Zygaenid moths might perhaps be justified. But Tothill's results in parasitising *Levuana* so successful that even Zygaenid eating birds would in any case destroy where parasitising has been effected far more of parasitised than of unparasitised larvae. If they selected parasitised larvae in preference to others, results of their introduction would be yet more harmful, and this is what has actually happened in case of South African locust-eating bird which has become injurious instead of beneficial as it specially attacks locusts which have been parasitised. In these circumstances Director represents that he would be strongly opposed to introduction of insectivorous birds Islands of Fiji as being a dangerous and at present unjustifiable experiment."

Several long telegrams were then exchanged between the Government and the Secretary of State, but the ornithological advisers in London believed that risks would be incurred in liberating the birds, and in deference to this advice, the project was reluctantly abandoned.

F.—Continuation of Search for Levuana and Allied Insects

In the discussion of previous work reference has been made (p. 6) to the strange distribution of *Levuana iridescens* and to the even more remarkable absence of parasites in its known range, both these peculiarities suggesting, although not proving, that the insect was not indigenous to Fiji.

It was clear that if a country of origin could be found there also could one hopefully look for controlling agents.

Studies by Tothill of a group of tent caterpillars of the genus *Malacosoma* in Canada—one species of which is confined to the Eastern provinces, another to the Western ones, while a third ranges across the continent—had shown that the principal parasites of the three species were identical, and this despite differences of form and habit greater than those between *Levuana* and *Artona* larvae. He was, therefore, of the opinion that it would be of equal practical value if insects closely related to *Levuana* could be found. Were Canada to undergo subsidence so that only the highlands remained above the sea, islands might be found having the first or the second or the third species of tent caterpillars. By analogy, as Melanesia probably represents a former continental area, if the original home of *Levuana* were in any part of that area, then the various island groups could be expected to yield various *Levuana*-like species. In 1925, of such species, *Levuana* in Fiji, and *Artona* in Java and Malay were known to science as well as some other species in Malay and Cochin China ; but as the intervening island groups had been but little searched we determined to seek *Levuana* or other related forms in them. Accordingly, in March 1925, Taylor was despatched to New Guinea and New Britain, and his searches were rewarded by finding four species of related Zygaenids with larvae that fed in the same peculiar way as *Levuana*. This visit coincided with the wet season, and although feeding scars on various species of Zingiberaceae were occasionally plentiful, yet living examples of the insects in any stage proved to be extremely rare. However, several species of important parasites were shown to be present, and although no bulk collecting could be done, the results obtained on this mission were most encouraging.

It had been the intention to continue the search through Cochin China, partly for the reason that *Artona*-like Zygaenids were known to occur there and partly for the reason that prior to the first record of *Levuana iridescens* in Fiji there had been a fairly extensive sandalwood trade between Fiji and southern China and there was the possibility that *Levuana* had been introduced at that time. This plan was interrupted by Mr. Taylor returning to Fiji with a shipment of *Artona* parasites, and then proceeding to Java to obtain additional parasites of *Artona* should they be required, and to study the parasites of related insects, and was finally not carried out.

On proceeding to Java, as mentioned above, Taylor again found a small group of *Artona*-like insects, and on this occasion he was able to obtain a considerable amount of information concerning their insect parasites.

In 1928, while Tothill and Paine were in the Solomon Islands on a mission not connected with *Levuana* they were nevertheless able to utilise odd moments in seeking *Levuana*-like forms and were rewarded by finding four species of *Artona* and *Levuana*-like insects, two of which are apparently similar to ones found by Taylor in New Guinea.

As a result of these three searches, we now know of nine Malayan or

Melanesian species of ZYGAENIDAE in the *Levuana-Artona* group, and we know that many of their parasites are common to several hosts. An account of this phase of the work has been written up by Taylor and will be found under the heading of "Allied Zygaenids and their Natural Control" (p. 210). This part of the work has proved to be of little practical advantage to Fiji except that perhaps it helped to restore confidence in the copra industry toward the end of 1925 by making it clear that even if *Artona* parasites should prove of no use we could try parasites of some of the others. To be sure, the island homes of several of these were less distant from Fiji than the Federated Malay States and the *Artona* outbreaks from which we obtained a wealth of *Ptychomyia* parasites, but none of these lately discovered Zygaenids were so numerically abundant as *Artona*, and their parasites could not have been obtained in such quantities. These discoveries have shown at least this, that *Levuana iridescens* is unlikely ever again to become a pest in any part of the ancient Melanesian continent. It has also shown that the classification of this section of the ZYGAENIDAE is in need of revision (cf. p. 37).

Though these searches have not settled whether or not *Levuana* is indigenous to Fiji, they have shown that a very close relative is found in the Solomon Islands and have added evidence tending to show that *Levuana* is probably not native in Fiji and that it probably occurs, or sometime in the past did occur, as a rare and highly parasitised insect in the New Hebrides or Solomon Islands. In this connection it is significant that each one of the nine allied insects now known between Java and Fiji, with the exceptions of *Levuana* and *Artona catoxantha*, are rare and highly parasitised, and even *Artona* is frequently in the same condition. *Levuana* in Fiji without parasites, and as an extremely abundant insect not in a condition of biological control, stands out in such strong contrast to its eight allies that it is more difficult than ever to believe that it is indigenous to Fiji.

G.—INTRODUCTION OF ARTONA PARASITES

Having followed out to its conclusion that part of the programme adopted by the Levuana Committee in January 1925 that had to do with searching in various island groups for *Levuana* and its allies, we will now follow up the decision made at the same time to make a third attempt to introduce parasites of *Artona catoxantha*.

Historical.—A brief statement of the circumstances that led up to the attempts to introduce the parasites of *Artona* has been made by the writer in Legislative Council Paper 71 of 1925, and the following is taken therefrom :—

> "*Artona*, or *Brachartona*, *catoxantha* has been known since 1892 as a sporadic pest of coconuts in Indo-Malaya, and there are a number of references to its parasites in literature. To give only a few, L. Lewton Brain said of a 1912 outbreak : 'The final checking of the spread of the pest was accomplished by a parasitic *Ichneumonid*, which was found present in large numbers at the height of the outbreak.' This was evidently the *Apanteles* that Messrs.

Simmonds and Taylor found so abundant this year (1925) at Batu Gajah. Burkill, in 1914, mentioned a Tachinid parasite in the Sirangoon outbreak of 1913, and P. E. Kuchenius, in 1916, mentioned a Tachinid as being important. The Clerid beetle, *Callimerus* sp., was mentioned for Sumatra as a useful predator on *Artona* by A. A. L. Rutgers in 1918 ; and a *Mesostenus* by W. C. van Heurn in 1921. There are also numerous references to a fungus disease, *Botrytis* or *Verticillium necans*, some cultures of which were introduced into Fiji at the instance of Mr. C. H. Knowles in 1921.

" So far as I have been able to discover the first suggestion to use *Artona* parasites against *Levuana* was made by Mr. C. H. Knowles in a letter to the Director of Agriculture at Kuala Lumpur written on 15th September, 1920. He says : ' We should esteem it a favour if you are able to give us any information as to the parasites of your Coconut Leaf Moth. . . . This moth has much the habits of, and is apparently very close to, our *Levuana iridescens* . . . and we feel that we should probably be well advised to attempt to introduce, if possible, certain of *Catoxantha's* enemies. . . . ' A year later Mr. H. W. Simmonds received a letter from Dr. G. A. K. Marshall under date of 23rd September, 1921, with the statement, ' I should think the experiment of introducing *Brachartona* parasites would be well worth trying.' It is quite possible that Mr. Knowles was advised in the first instance by Dr. Marshall, but I have so far been unable to find any correspondence on this point. More recently Messrs. Simmonds and A. M. Lea have both advocated bringing in the *Artona* parasites."

Reasons for considering these Parasites to be Important.—Prior to 1925 *Artona catoxantha* was the only ally of *Levuana* known in the Malayan Melanesian regions that could be considered of importance as a source of parasites. On the basis of adult characters on which the classification of the group has been made, *Artona* is so far removed from *Levuana* as to be placed in a different sub-family. On the other hand, the larvae of *Levuana* and *Artona* are very much alike, and feed in an almost identical manner upon the leaves of the coconut palm. As parasites attack the larval stage, it seemed sufficiently probable that parasites of *Artona* would attack *Levuana* to justify another attempt at introduction in spite of dissimilarities between adults. Tothill's studies on natural control of Canadian insects made him anxious to push this part of the programme vigorously, and the public and the Levuana Committee had heard so much of Hawaiian successes in such measures as to make them almost equally enthusiastic.

Decision to attempt the Introduction of Ptychomyia and Apanteles.—Several parasites of *Artona* were known, and it was necessary to confine the initial effort to one or possibly two species because it was almost inevitable that each species dealt with would require a different routine on shipboard. The Government Entomologists in the Java and the Federated Malay States had shown that *Ptychomyia* and *Apanteles* were probably the most effective parasites, and it was decided, therefore, to concentrate upon these two, and particularly upon *Ptychomyia* for the reason that it was probably the most difficult of all to bring to Fiji. As our terms of appointment were initially for two years only, it seemed prudent to make an early start with the most difficult species.

Difficulties.—The two-winged fly, *Ptychomyia* (Plate XXXII), belongs to the family TACHINIDAE, most of whose members have proved to be very difficult to breed in captivity. Tachinid flies had been taken from Europe to America in the Gipsy and Brown Tailed Moth campaign, but the journey was completed in ten days and they could be sent as internal parasites within their caterpillar hosts. A related fly called *Crossocosmia sericariae* had been taken from Japan to Boston, U.S.A., but in this case distance was no obstacle because the species normally hibernated, was accustomed to freezing temperatures, and could be transported without harm in a refrigerator. Mr. F. Muir was able to save the sugar industry of Hawaii by transporting a Tachinid fly from Java, but in this case the difficulty was overcome by establishing two relay breeding stations, one in Queensland and one in Fiji, so that the actual journey for any one batch of flies was reduced to approximately ten days.

A difficulty in the case of *Ptychomyia* was that on account of it being a tropical insect and having no hibernating period it could not be shipped in cold or even cool storage. A relay station in Queensland was out of the question on account of the risk of introducing *Artona* or *Levuana*, one of which would have had to be used as a food supply. The remaining alternative was shipment to Fiji in an active condition either by way of Australia or by direct freight boat. Via Australia was unsatisfactory for two reasons, namely, the danger of introducing *Artona* or *Levuana* and because shipment would have to be limited to the Australian summer months which might not coincide with *Artona* outbreaks. For practical purposes, therefore, it was expedient to attempt direct shipment. Aeroplanes were not available, and the cost of chartering either a fast naval vessel or merchant ship for the 4,000-mile journey would have been prohibitive. Our only hope was an occasional freighter, and it would therefore be necessary to keep *Ptychomyia* alive for not less than twenty-three days. A further difficulty lay in the fact that, including the vessels bringing indentured and free Indian labour to Fiji, there are frequently only one or two freight boats in the year coming direct to Suva from Singapore or Batavia. Moreover, the outbreaks of *Artona* in Java and the Federated Malay States were few and far between, and only those could be utilised in which parasitised larvae of the right age occurred at the time a vessel could call.

Mr. H. W. Simmonds sent to the Federated Malay States.—It was not without anticipation of difficulties that Mr. Simmonds was sent to Kuala Lumpur to await an outbreak of *Artona* from which parasites could be obtained in the right stage to permit of shipment by one of the few available freight boats. The serious position on Ovalau, however, justified the risk of a third failure.

Discovery of the Batu Gajah Outbreak.—For the first three months of Mr. Simmonds' mission there, no outbreaks occurred. In the meantime Mr. Taylor had been on his mission to New Guinea, and it happened that as he was passing through the Federated Malay States en route for Cochin China a small outbreak of *Artona* was discovered—thanks to the active co-operation of the local entomological staff and their field inspectors—at Batu Gajah. The outbreak was confined to a few acres of land, and there were only a few trees present, but as examination showed that both *Ptychomyia* and *Apanteles* were present the Committee decided to attempt a shipment if transport to Fiji could be arranged. Mr. Taylor was asked to remain in the Federated Malay States so as to assist in the difficult task of assembling the shipment, and as Mr. Simmonds was soon to proceed to England on long leave, it was also arranged for Mr. Taylor to escort the shipment to Fiji.

Arrangements for assembling the Shipment.—On account of the long journey Simmonds and Taylor were instructed to make a very large shipment under as natural conditions as possible in the hope of getting a small percentage of the parasites through alive.

To this end cages were designed 5 ft. tall, 3 ft. wide and 4 ft. long, made of dressed lumber, the upper part to be fitted with very fine wire gauze (eighty-five meshes to the inch) to prevent the escape of secondary parasites while allowing ventilation. Glass windows and canvas screens were also fitted so that ocean spray could be shed in case of rough weather on the voyage. The cages were also provided with removable poles to enable them to be lifted by a labour party. Seventeen such cages were used in the shipment, and variations were made in some. In two, for instance, double doors were arranged to facilitate examinations en route and particularly to aid in the preparation of clean cultures without secondary parasites.

As soon as Mr. Simmonds had arrived at Kuala Lumpur, he made arrangements for about 100 newly sprouted coconuts to be planted in those useful articles ubiquitous in the tropics, the four-gallon kerosene or benzine tins. Four or five such tins could be accommodated in each cage, and the plan was to load each coconut leaf in most of the cages with parasitised larvae of *Artona* and to load the remainder with unparasitised larvae to be used as a food supply for the parasite generation emerging en route. This plan was not adhered to exactly, because in the rush of loading the leaves with *Artona* larvae at the latest possible hour prior to sailing it happened that both parasitised and unparasitised larvae, the latter of several ages or instars, were depastured in a number of the cages.

In making these collections advantage was taken of the fact that usually, even without a hand lens, it was possible to distinguish an *Artona* larva parasitised by *Ptychomyia* from ones not so parasitised, so that a great concentration of parasitised larvae could be arranged in the cages.

The one almost insurmountable difficulty not provided for in these arrangements was that in the Batu Gajah outbreak there was very little overlapping of the stages of *Artona*, and as *Ptychomyia* attacked chiefly fourth and fifth stage larvae, it was not found possible to provide sufficient hosts in the right stage for all the flies emerging en route. Chiefly for this reason, it was estimated that only five living flies were likely to arrive at Suva for each 100 parasitised *Artona* larva placed in the cages in Malay, and the shipment was consequently made large enough to justify an expectation of 500 living flies in Suva.

Shipping Arrangements.—The Clan Line of cargo boats ply between London and Fiji and sometimes come by way of Singapore. On June 9th, 1925, the owners of this line, Messrs. Cayzer, Irvine and Co., advised their local agents, Messrs. Brown and Joske, that the *Clan Mackay* could call at Singapore in the early part of July, that she was due to call at Cairns in Queensland for 1,000 tons of ore and at Brisbane for 1,500 tons of bunker coal. As each day of delay between Singapore and Suva lessened the chances of bringing parasites through alive an effort was made to induce the vessel to bunker at Singapore, but this could not be arranged. The delays might make the difference between success and failure, but we could not be sure of another direct boat for several months, and in view of the ravages of *Levuana*, the Committee decided to accept the considerable risk of a third unsuccessful attempt to introduce *Artona* parasites.

On June 17th notice was received that the *Clan Mackay* would call for the parasites at Singapore about July 4th, and instructions were sent to Simmonds and Taylor to prepare the shipment. This date suited admirably, because the *Artona* larvae at Batu Gajah were in the fourth and fifth stages just prior to this date, these being the stages chiefly parasitised by *Ptychomyia*. Arrangements were almost complete when advice was received that the vessel would be delayed about a week on account of having to go to the assistance of another vessel in distress. Had the delay been for two weeks it would have been impracticable to attempt a shipment, and although the delay of one week measurably reduced the chances of success, it was decided to carry out the attempt.

Instructions to load the larvae on to the palms were sent to Mr. Simmonds on July 8th, the vessel being due to leave Singapore on July 10th. As Batu Gajah is roughly three hundred miles by rail from Singapore, it was necessary to conduct the operation with the utmost expedition. Thanks to careful organisation, however, matters went forward rapidly and without a hitch, approximately 20,000 *Artona* larvae were duly loaded on to eighty-five young palms which were placed in seventeen wooden cages and railed to Singapore in time to catch the boat.

While the loading had been going on in the Federated Malay States, the Committee in Suva had been able to effect an improvement in the shipping arrangements whereby, for an additional £250, the entire steamer charge being £750, a saving of at least three days was effected.

On July 9th, at 10 a.m., a cable was received advising that owing to unexpected circumstances the *Clan Matheson* was sailing direct from Java to Suva on July 10th—the same day on which the *Clan Mackay* was leaving the nearby port of Singapore for Suva via two Australian ports. At 11 a.m. the Committee despatched the following uncoded message at urgent rates to the Managing Director of Cayzer, Irvine and Co. in London :

> "Surabaya advise *Clan Matheson* sailing 10th July Suva direct. In view extreme importance to coconut industry which provides your cargoes and short life parasites Government urgently request detain *Clan Matheson* Surabaya divert *Clan Mackay*. Government willing pay reasonable demurrage up to another £250."

London is on the other side of the international date line from Suva and also nine hours of longitude distant, and this cable was therefore due to reach London at 2 a.m. on the night before it was sent as reckoned by Suva time. It is unlikely that it was dealt with until eight or nine hours later, but within twenty-three hours of sending the message the following favourable reply was received at Suva and both vessels had been notified :—

> "*Clan Mackay* have instructed steamer call at Surabaya to transfer parasites to *Clan Matheson* will agree to £250 extra although does not cover demurrage expenses."

This action on the part of Messrs. Cayzer, Irvine and Co. was appreciated highly.

At about 11 p.m. of the second day out from Singapore the *Clan Mackay* anchored in Surabaya harbour and transferred Taylor and his parasite shipment by means of a lighter to the *Clan Matheson*, which ship immediately put to sea for Suva.

The voyage was uneventful except that a head wind between Thursday Island and Fiji caused the Captain to take the Townsville track and resulted in a delay of about two days, the steamer actually arriving in Suva harbour early on August 3rd, the parasites having been collected twenty-five days previously at Batu Gajah.

Arrival at Suva.—In the meantime an insectary had been built in Suva for the purpose of receiving the parasites and of preventing the escape of secondary parasites and also of *Artona* itself. This little building had been made with great care as the escape of one fertilised female of any secondary parasite might reduce considerably the effectiveness of *Ptychomyia*. It was furnished with the usual double doors with lobby between ; it was screened with a copper bronze gauze having sixty-five meshes to the linear inch ; and was set up on posts arising from a concrete cup of water to prevent the passage of ants.

The various attempts to introduce *Artona* parasites had now cost in the neighbourhood of £3,500, and the Committee was naturally anxious to know, first, whether any parasites had survived the voyage ; and, if so, whether they would attack *Levuana*. In respect to the first point, wireless messages had reported that although most of the parasites were dead there were still a few living ones in most of the cages.

The cages began to arrive at the insectary by 9 a.m. on August 3rd, and by 10 p.m. that evening all had been examined once. Approximately 300 active *Ptychomyia remota* adults were taken from the cages and placed in three fresh cages previously constructed to receive them. In the cages a supply of fourth and fifth stage *Levuana* larvae had previously been assembled, and the flies immediately attacked them as to the manner born.

Before continuing this account of the Tachinid fly, it may be said here that the cages yielded nothing but these *Ptychomyia*, some secondary parasites thereof and some predacious beetles known as *Callimerus arcufer* that were subsequently bred up and liberated at a number of points throughout the Colony. There were hundreds of empty pupal cases of *Apanteles*. The adult *Apanteles* (cf. Plate XXXIV) had all emerged but had found no *Artona* at the right age for attack, and so had died without perpetuating themselves. A more or less technical account of the beetle is given later (p. 249), and it is sufficient to say here that, although many colonies have been liberated, the beetle has not yet been recovered from the field, and it may or may not be established. The Malay cages were fumigated as soon as the adult *Ptychomyia* flies were removed in order to kill any *Artona* larvae which might have survived. All the secondary parasites were also immediately destroyed. These secondaries or hyper-parasites which live within the *Ptychomyia* larvae as the *Ptychomyia* larvae live within the Zygaenid caterpillars detract considerably from the efficiency of *P. remota* in Malaya, and had any been allowed to escape in Fiji the victory over *Levuana* might have been much less prompt and decisive than it has proved to be.

The Breeding of Ptychomyia.—The exact number of *P. remota* individuals which came through alive was 315—all adults. These flies, transferred from the Malay cages to clean Fiji cages on August 3rd, formed the entire basis of our breeding stock. All these Malay adults were kept in a large cage inside the insectary, and during the afternoon of August 3rd they showed most convincingly that they would oviposit on *Levuana*.

It had now been proved that the fly would attack *Levuana*. There is a difference, however, between an attack and a successful attack, because there are on record a number of cases in which an unaccustomed host is liable to destroy the invading parasites by means of its large motile blood cells, called phagocytes. These accumulate around and destroy the invading parasite, the process being known as phagocytosis.

By the evening of August 4th we had 263 parasitised *Levuana* larvae; and at the end of a week this number was increased to 868. During the succeeding few days the early stages of the parasite were watched carefully, and after seeing that the larvae had successfully bored into their new host, we obtained the first puparium on August 11th, and on August 21st had the gratification of seeing an adult *Ptychomyia* fly emerge, which gave positive proof that this parasite was capable of breeding successfully on *Levuana*.

The adult flies were laying so readily in captivity and large supplies of *Levuana* larvae were so easily obtained in and around Suva that it was decided to continue breeding the species in captivity rather than liberate our comparatively small stock immediately. Although we did on two occasions sustain very heavy losses in the breeding stock before starting to liberate any colonies, the cause of the trouble was remedied; and the routine method of breeding finally adopted was so successful that after five months we had bred 15,212 flies in captivity, and liberated parasite colonies over the greater part of the *Levuana* infected districts.

Rearing Difficulties.—So few Tachinid flies have been reared successfully in captivity that it may be of value to record the very simple cause of a mortality that almost exterminated the entire stock of flies on two separate occasions.

In the first instance the stock of flies had been bred up to 505, when on going to the cages on September 4th practically every adult fly was lying on the floor of the cage in a dead or dying condition. Instead, therefore, of being in a position to liberate the first colony we were reduced overnight to practically the position of a month before when the total stock consisted of about 300, but this time the stock consisted chiefly of " Tachinised " larvae rather than of adults. At the time we were unable to account for the sudden mortality. The honey used as food and the dead flies were analysed for possible poison ; the flies were examined for bacteria ; every step of the routine was examined with the greatest care, but all to no avail. On the facts it seemed possible that one of the feeding cloths had been used without being previously boiled, that alcoholic fermentation had been set up, and that the deaths were due to alcoholic poisoning.

The 300 " Tachinised " *Levuana* larvae yielded up their adult parasites and all went well again for a month, when this experience was repeated. By this time, however, we had a much larger stock of " Tachinised " larvae on hand and the loss of the adults was not so serious a matter. Up to this time the fly cages in the insectary had been arranged so that a spot of sunshine might fall upon one corner of them, as the flies appeared to appreciate it. Knowing how easily adult insects succumb to overheating, we tried eliminating this direct sunlight in case it might be the mysterious cause of the trouble, and from that day on there were no further losses. Above the woodwork the cages consisted for the most part of wire screen or Brussels netting, but at one end were some panes of glass to facilitate an examination of the cage from the outside, and there were also some panes of glass in the insectary. It now seems almost certain that on these occasions the direct sunshine passing through this glass was too powerful for the flies attracted to it. We had found that the flies laid much better where the light was fairly intense inside the cages, *i.e.* on a bright sunny day, and in our eagerness to get the maximum number of eggs, we had subjected the cages to an overdose of sunshine.

Routine finally Adopted.—The breeding cages described above (cf. Plate XIV) were used throughout, and proved most satisfactory, *i.e.* wooden cages 6 ft. high by 5 ft. by 3 ft., with a glass window at one end, and calico or Brussels net panels in the sides, door and roof. This allowed one to stand up inside the cages, and, when the latter were arranged so that the maximum light fell on the side, or, so long as direct sunlight were avoided, on the glass window end, it was possible to move in and out of a cage without fear of releasing many parasites.

Until two generations had been bred through, and it was quite certain that a pure stock of *P. remota* remained with no hyperparasites, we kept our breeding cages inside the insectary.

We were faced with the problem of feeding the parasitised caterpillars in captivity for several days after they were stung ; this was conveniently done by loading them on to seedling palms which we refer to by the convenient native name " vara "—potted up in empty kerosene tins. As the leaf surface on each vara was not sufficient to keep several hundred fifth-stage *Levuana* larvae alive for many days, it was essential to have a large supply of varas constantly on hand.

The adult flies were kept inside the insectary in a large cage and were fed twice daily with diluted honey on a cloth pinned up inside the cage. In addition to food the flies were watered regularly by spraying the inside of a cage twice or more times a day. A potted vara well loaded with *Levuana* larvae (fourth and fifth instar larvae only were used) was placed in a fly cage; the parasitised larvae were removed at least twice a day to prevent wastage of eggs by superparasitism, and the supply of healthy larvae renewed. Parasitised larvae were collected in a tube inside a fly cage, counted, and the number entered up on a special form at the office, where a record was kept of the output from each cage. The parasitised larvae were then loaded on to other varas and placed in cages outside the insectary. These larval cages were also sprayed twice a day during the week before the parasites were due to emerge in order to keep the parasite puparia moist.

Thus the day's routine consisted at first of:

(*a*) Renewing food for adult flies, and spraying with water (twice).
(*b*) Removing parasitised larvae from adult cages (twice).
(*c*) Replenishing supply of healthy larvae in adult cages (as occasion demanded).
(*d*) Renewing *Levuana* food supply in adult cages (as occasion demanded).
(*e*) Checking up numbers of stung larvae.
(*f*) Loading the parasitised larvae on to new varas and placing the latter in labelled cages outside the insectary.
(*g*) Spraying the pupae in the larval cages within a week of first expected emergence date.
(*h*) Removing any adults which had emerged in the larval cage, checking numbers and transferring them to adult cages.

This was quite a simple routine: and after the first eight weeks our native assistant, Jacobi, became quite conversant with the methods and carried out much of the work alone.

Two hundred adult flies were found to be sufficient to parasitise as many *Levuana* larvae as we could conveniently procure from day to day, so that after maintaining a supply of approximately 100 flies in each of two adult cages, all the remaining parasites were available for liberation.

On October 10th, 429 parasitised *Levuana* larvae were removed from the adult cages. This was the highest number ever obtained in one day.

A careful check was kept on the yield of adults from each cage of the first two generations. The percentage emergence of adult flies (*i.e.* out of every 100 parasitised *Levuana* larvae put in) from the first fifteen cages was as follows: 47, 45, 53, 58·5, 74, 81, 60, 59, 55, 65, 60·5, 54, 37·6, 42·5, 66—an average yield of 57·2 per cent. It is interesting that the highest yield, 81 per cent., was obtained from a cage which had been kept solely for larvae on which more than one parasite egg was laid.*

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* See Superparasitism, p. 205.

Liberation of Colonies.—By January 20th, 1926, less than six months from the arrival of the parasites in Fiji, colonies of the fly were distributed all through the *Levuana* infected districts, after which breeding in the insectary in Suva was concluded.

During the last month of colony distribution from January 20th to February 18th parasitised *Levuana* larvae were collected at Nasese, where the fly was well established.

Altogether thirty-eight colonies of *P. remota*, with a total of 32,621 flies, were liberated. The date of each liberation, strength of the colony and site of liberation are shown in the Table on p. 26. The map, Plate VIII, shows the initial distribution of the Tachinid colonies.

There seems not the slightest doubt that had we liberated colonies of as few as twenty flies instead of 700, *P. remota* would have become almost as rapidly established, so readily did the parasite adapt itself to field conditions in Fiji.

The first intimation of its real capabilities in the field was received on October 1st, 1925, when, after breeding for less than two months, the few flies which had emerged from discarded palms outside the insectary had started to attack *Levuana* on some nearby trees. On this date we discovered, amongst larvae collected for loading the palms in the fly cages, a few with parasite eggs already on them.

From the beginning of October the dispersal of the parasite in Suva and the surrounding district was watched most carefully, and it was remarkably rapid. On Plate VIII is a sketch-map illustrating subsequent recoveries of the parasite on trees at a stated distance from the insectary whence they had spread.

Our original plan was to liberate 1,000 individuals in each colony ; but in view of the rapidity with which the fly was spreading in Suva from only a few flies not expressly liberated, it was decided to cut the original figure to about 700 parasitised larvae, giving an adult yield of about 500.

As the rate of production of parasitised larvae was about 250 a day during most of this time, it took only three days to provision a colony. Thus by transporting colonies to the desired site about a week after the palms were loaded up with parasitised larvae most of the latter would have spun their cocoons, and could be conveyed to the desired site with the minimum risk of loss during the voyage. The adult parasites would emerge over a period of not more than a week, the majority during a period of three days only. This method of liberating colonies proved quite satisfactory and was adopted throughout.

At first it was thought advisable to take elaborate precautions to protect the colonies on the palms from ants, and for the first few colonies a wooden stand was constructed (Plates XIV and XV), the legs of which were ringed with tangle-foot. It was later decided that this was going to unnecessary trouble, and in distributing the later colonies the tins of palms with the parasites were just stacked together beneath a coconut tree well provisioned with *Levuana*.

COLONIES OF PTYCHOMYIA REMOTA LIBERATED IN FIJI, 1925–26.

	Site of liberation.	Date of liberation.	Strength.
1.	Suva	Aug.–Sept. 1925	50
2.*	Caboni (Ra)	7.x.25, 9.ix.25	1274
3.*	Nanuku (Ra)	27.x.25	1470
4.†	Loreto (Ovalau)	5 and 11.xi.25	2205
5.*	Naigani	22.xi.25	1588
6.	Niubasaga (Moturiki)	21.xi.25	833
7.	Namuka	3.xii.25	751
8.	Draubuta (Lower Rewa)	9.xii.25	704
9.	Vunisinu ,, ,,	9.xii.25	788
10.	Nabitu ,, ,,	9.xii.25	700
11.	Laucala ,, ,,	21.xii.25	720
12.*	Naililili ,, ,,	19.xii.25 21.i.26	1480
13.	Waitovu (Ovalau)	21.xii.25	700
14.*	Cawaci ,,	21.xii.25	1400
15.	Vuma ,,	21.xii.25	700
16.*	Rukuruku ,,	22.xii.25 30.xii.25	1400
17.	Cawatara ,,	22.xii.25	700
18.†	Bureta ,,	22.xii.25 31.xii.25	2100
19.	Levuka ,,	29.xii.25	700
20.	Nacobo ,,	29.xii.25	700
21.	Lovoni ,,	31.xii.25	700
22.	Nagara	31.xii.25	700
23.	Naitonitoni	31.xii.25	700
24.	Sawani (Waimanu)	10.i.26	535
25.	Cuvucuvu (Nausori)	10.i.26	214
26.	Batiki ,,	10.i.26	214
27.	Navutoka ,,	10.i.26	437
28.	Verata ,,	12.i.26	700
29.	Nasesara (Moturiki)	12.i.26	700
30.	Savuna ,,	12.i.26	700
31.	Daku ,,	12.i.26	700
32.‡	Lawai (Sigatoka)	25.i.26	2800
33.	Lawaki (Lautoka)	27.i.26	700
34.	Navioga ,,	28.i.26	700
35.	Teidamu ,,	28.i.26	700
36.	Nacewa (Beqa)	18.ii.26	160
37.	Kavaga ,,	18.ii.26	26
38.	Raviravi ,,	18.ii.26	222

* Two colonies liberated in same locality.
† Three colonies liberated in same locality
‡ Four colonies liberated in same locality.

Rate of Dispersal.—In the tropics, where breeding is not interrupted by a winter season, one can expect the rate of dispersal of an introduced Tachinid fly to be greater than in temperate climates. In the case of the fly, *Compsilura concinnata*, introduced from Europe first into Massachusetts and later into Canada, a period of approximately five years elapsed after the initial introduction and before the species became common in the Gipsy and Brown Tailed Moth areas, and in the case of another fly, *Blepharipa scutellata*, the period was much longer. One could expect *Ptychomyia* to do better than this in Fiji, but we had not ventured to hope for anything like the astonishingly rapid rate of distribution that culminated with its spread throughout the *Levuana* zone in Fiji by April 1926, or six months after the liberation of the first colony in October 1925. The rate of dispersal from a single point is best illustrated by the record at Suva.

Dispersal at Suva.—Our record for the Suva district is more complete than for any other because Tothill and Paine had headquarters there and made frequent examinations of *Levuana* larvae in the immediate neighbourhood. Also, as we were using hundreds of larvae daily collected from various parts of Suva for the breeding work, and as these were automatically handled individually in their passage through the cages, they were of great assistance in checking the spread of the fly. This colony was also the most natural one in Fiji because instead of having originated from the liberation of 700 Tachinised larvae estimated to yield 500 adults, it resulted from six recorded escapes of adults at the insectary door plus an estimated number of two dozen flies that had emerged over a period of weeks from discarded palms that had been used in the breeding cages, and from which all the visible "Tachinised" larvae had been carefully collected. Our record can be condensed as follows :—

(t.l. means "Tachinised" larvae.)

Oct. 1st, 1925.	Found 4 t.l. close to the insectary (within 100 yards of site now occupied by Government House).
,, 22nd ,,	All palms close to insectary examined ; found t.l. thinly distributed on 12 of them.
,, 27th ,,	Found t.l. very thinly distributed on 8 of the little palms in Government House Grounds close to the Native Rest House (at present used as a Museum).
,, 28th ,,	Found t.l. at Nasese "very thinly" but evenly distributed between the halfway point on the straight part of the Nasese Road to the eastern end where it bends at right angle. This is from ¼ to ½ a mile from the point of liberation.
Nov. 26th ,,	Found t.l. in the grounds of the Doctor's quarters at the Suva Memorial Hospital. About 2 miles from the colony site.
Dec. 7th ,,	Collected 915 t.l. at Nasese about ½ mile from colony site. Estimated the parasitism on 4th and 5th instar larvae to be between 50 per cent. and 90 per cent. A note in Tothill's diary reads : "This day marks the beginning of a new phase in which collecting from the field may supersede cage breeding."
,, 17th ,,	Found t.l. at Lami "very thinly" distributed. Absence on trees along the shore between the colony site and Lami indicates probability of the insect having flown about 3 miles across the harbour.
,, 29th ,,	Found t.l. at top of hill east of Nasese (about 1 mile from insectary) on Flagstaff Hill (about 1 mile) ; along the Point Road to within ¼ mile of "the Point" (2½ miles from insectary) ; and in the garden of the Overseer's house P.W.D. depôt at Tamavua (3½ miles). None found near the Government Rice Mill, near the Gaol, or between "the Point" and Tamavua.
Jan. 13th, 1926	Found t.l. at the Samabula Rifle Range (4½ miles from the colony site).

Reasons for the Rapidity of Spread.—Apart from the continuity of breeding possible in the tropics, to which reference has already been made, there are four other factors that have played an important part in the rapidity of distribution. These factors are :

(*a*) The strong flying powers of *Ptychomyia*.
(*b*) The overlapping of broods of *Levuana*.
(*c*) The absence of secondary parasites.
(*d*) The enormous quantity of *Levuana* available.

(*a*) *Powers of Flight of* Ptychomyia.—A large amount of information has been collected concerning the powers of flight of the common house fly, which to look at is a very similar sort of fly to *Ptychomyia*. This information has been obtained by releasing at a given point a number of flies lightly sprayed with one of the very sensitive indicators that turn a bright colour in the presence of an acid. Flies are then trapped on sticky papers at various distances from the point of liberation, and the sticky papers are then run through an acid bath, when any of the liberated flies take on the colour for the particular indicator used. In this way flies have been found to travel half a mile with considerable frequency and a mile not uncommonly.

In the case of most Tachinid flies, however, information as to length of flight is very meagre. One of the few records known was made by Tothill in the case of *Compsilura concinnata*. Flies had been liberated at Fredericton, N.B., in Canada, and a short time afterwards their progeny were dissected from some Fall Webworm (*Hyphantria cunea*) larvae collected three miles from the point of liberation across a river that was half a mile wide. For *Ptychomyia* we have many records, some of them much longer flights than the one mentioned. The seeming record of a three-mile flight across Suva harbour is open to the objection that the fly may have gone round the coast in easy stages in spite of our failure to find any Tachinised larvae at intervening points. The first convincing flight record was established as a result of finding *Ptychomyia* on Viti Levu at a point at least half a mile distant across open water from a colony established on the island of Namuka. After this record it was not surprising to find the insect on the islands of Nukulau and Makuluva, involving minimum flights across open water of about three-quarters and half a mile respectively. The first real surprise came when we found the fly established on the island of Yanuca, which is seven miles from the nearest island of Beqa (Mbenga) on which was the nearest colony. The most interesting record of all resulted from the finding of the fly on the tiny little coral island of Navini ; in this case the fly could have come only from Viti Levu, the nearest part of which was twelve miles distant across open water.

(*b*) *The Overlapping of Broods of* Levuana.—Another factor that had a great deal to do with the rapid dispersal of *Ptychomyia* was the overlapping of the *Levuana* broods prior to the arrival of and during the first few months of the presence of *Ptychomyia* in Fiji. On account of this overlapping one could frequently find eggs, the five larval stages, pupae and adults of the moth on the same tree at the same time. The fly attacks only third, fourth, and fifth-stage larvae, and chiefly the latter two, and it completes its life cycle in less time than does *Levuana.* On account of the overlapping of broods when the flies emerged in waves from fourth and fifth-stage larvae, there were others at the right age for attack, and consequently multiplication of the flies proceeded at a very rapid rate indeed, generation succeeding generation with no check from food shortage—at least during the first few months.

(*c*) *The Absence of Secondary Parasites.*—In Malay there are several parasites that prey upon *Ptychomyia* and reduce its effectiveness in consequence. The long voyage and the subsequent reduction to pure cultures in the insectary enabled the secondaries to be killed off, and the consequent absence of secondary parasites in Fiji appears to have been a contributing factor in the rapid spread that took place.

(*d*) *The Numerical Abundance of* Levuana.—When the Suva colony was liberated, there were few coconut trees in the Suva district without *Levuana ;* on most of the affected trees the insect was abundant, and in a few acres of trees at Nasese an outbreak was in full progress, so that no matter in what direction *Ptychomyia* turned there was abundant food material. In the few acres of trees at Nasese alone it is estimated that there were upwards of a million larvae available for attack, and there is little doubt that the rapidity of dispersal was aided to a large extent by this abundant food supply.

General Dispersal in the Colony.—The rapid dispersal in Suva proved to be more or less typical for the whole of that part of Fiji infested by *Levuana.* We believe that of the thirty-eight colonies liberated only one failed to establish itself, namely, the one at Nanuku, where a *Levuana* outbreak died out too quickly on account of defoliation of the palms, and a consequent starvation of *Levuana* occurred. Numerous outbreaks of *Levuana* were in progress, and by April 1926 recovery of *Ptychomyia* had been made from such a representative list of places throughout the infested area, including isolated trees in the centre of Viti Levu and an island of about an acre in extent twelve miles off the coast, as to render it highly probable that by this time the fly was completely dispersed throughout the *Levuana* area.

The Effect of Ptychomyia.—The first indication of what this fly might accomplish was noted at the site of liberation of the Suva colony. Within three months of liberation the parasitism on two trees became so high that *L. iridescens* was exterminated. Progress of the fly in the Nasese outbreak was therefore followed with the greatest interest. In Canada Tothill, Baird and Dustan had found in the case of five common Lepidopterous insects that their parasites exerted a maximum pressure in the periods between outbreaks and had the effect of lengthening these periods. In the case of an actual outbreak of these Canadian insects, the parasites had proved unable to exert control until the food shortage stage of the host plants had been reached.

It came as an agreeable surprise, therefore, to find the percentage of parasitism mounting rapidly in the Nasese outbreak until it reached anywhere from 50 per cent. to 100 per cent. on the pupae, with the percentage varying somewhat from tree to tree. This had the effect of preventing a flight of moths from the main block of trees across a small tidal creek to a further acre of trees, and on these trees, where *Levuana* was present but had not reached outbreak strength, the fly completely eliminated the insect. The effect was remarkable, because on one side of the creek the trees were gloriously green and on the other, where defoliation was nearly complete at the time the fly reached maximum abundance, the trees were ashen grey.

These two achievements of cleaning up *Levuana* on isolated and not heavily infested palms, and of preventing a flight of moths from an outbreak area made it possible that *Ptychomyia* alone would be able to control *L. iridescens* throughout Fiji.

Position Six Months after the Introduction of Ptychomyia.—Six months after the initial introduction of *Ptychomyia* this remarkable fly was estimated to have spread throughout that part of Fiji affected by *Levuana*, and in many places it brought about similar conditions to those recorded above for Suva and particularly for Nasese. Many of the outbreaks had subsided entirely, and *Levuana* had even disappeared from a fair percentage of isolated trees in native gardens.

Although the progress made toward the control of *L. iridescens* appeared to be most promising, a new stage was now entered upon and the future could not be foretold with any degree of certainty.

(*a*) *Elimination of the Overlapping Broods.*—Reference has been made already to the existence, prior to the introduction of *Ptychomyia*, of overlapping broods of its host which had the effect of providing a complete larder of *Levuana* for the first few generations of the fly, which in turn enabled the fly to multiply with extraordinary rapidity. When the parasitism reached 70 per cent. and over, however, some broods became nearly or completely eliminated until a time came when flies emerged to find no *Levuana* larvae in the right stage for attack. Such flies had to find their way to other places where *Levuana* was in the proper stage, or to find secondary hosts, or to die without ovipositing. In places, therefore, *Levuana* began to recover from the initial shock, and the question of whether or not secondary hosts were to be found in Fiji became one of absorbing interest.

(*b*) *The Question of Secondary Hosts.*—In Malay Gater * has recorded three hosts of *Ptychomyia* :

1. *Artona catoxantha.*
2. *Achaea janata.*
3. *Sylepta derogata.*

In Java Taylor has reared it from :

4. *Artona trisignata.*

In Fiji we reared the fly from :

5. *Levuana iridescens.*
6. *Plutella maculipennis.*
7. *Eublemma* sp.

Under laboratory conditions it has also been bred in Fiji from :

8. *Callimerus arcufer.*
9. *Agonoxena argaula.*
10. *Sylepta derogata.*

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* *Malayan Agric. J.*, xiii, 1925, p. 113.

In the field numbers 8 and 9 can be discounted, because under natural conditions the larvae of both live hidden from the fly. The only known secondary hosts of practical value in Fiji, therefore, were numbers 6 and 7.

Plutella maculipennis (6) feeds on cabbage, which is, of course, an introduced plant and cultivated by few, mostly Chinese, in market gardens about Suva, Lautoka and other settlements. *Eublemma* sp. (7) feeds on the raintree, *Albizzia lebbek*, also an introduction but now fairly well distributed in the Colony. If *Ptychomyia* were confined to these two species aside from *Levuana* as hosts in Fiji, the Levuana Committee would have advised the increase of cabbages or raintrees or both, throughout the Coconut areas, or might have considered the introduction of one of the harmless *Levuana*-like species which were found in New Guinea or the Solomons feeding on plants of the Zingiberaceous genus *Alpinia*—a genus well represented in the native bush of Fiji. But though we have not yet succeeded in rearing this parasitic fly from any insects belonging to the little-explored bush fauna of Fiji, we have reason to believe that some such hosts must exist in addition to the species from which we have succeeded in rearing it. We have arrived at this conclusion as a result of planting out trap larvae of *Levuana* in places where the insect was practically exterminated and afterwards examining them for eggs of the fly.

On May 1st, 1926, when *Levuana* had become extremely difficult to find in the Suva district, a hundred fourth-stage larvae were obtained elsewhere and placed on a coconut tree in the Presbyterian churchyard. On the following day sixty-three had been attacked by *Ptychomyia*, and on May 3rd the percentage was increased to sixty-eight, thus showing that the fly was still abundant despite the scarcity of *Levuana*.

Here we might mention that in order to keep an adequate supply of healthy *Levuana* larvae for experiments in connection with the introduced predator, *Callimerus arcufer*, we found it necessary to screen in the whole of a young coconut tree in Government House grounds.

In November a similar experiment was made on Ovalau, where the *Levuana* position has been followed closely. In March a big outbreak had been in progress, but the fly had become sufficiently numerous to prevent moth flights. Toward the end of April the outbreak had been brought under control, and by the end of September, when the trees had recovered to the extent of having four to nine green leaves at the top, Paine and Tothill were unable to locate any " carry over " trees with the aid of glasses. Fourteen of the most likely looking trees from various places round the island were felled. Only one had *Levuana* present, and in this case there was a 60 per cent. parasitism, so that *Levuana* had become extremely thinly distributed.

In November Paine could find no *Levuana* at all, and it was clear that *Ptychomyia* could no longer be present in any numbers unless secondary hosts were fairly abundant. Eggs of *Levuana* could be collected at the time from the little island of Leleuvia, and on November 14th 300 eggs were planted out at Lovoni in the centre of Ovalau far from raintrees and cabbages. These hatched, and twenty-seven larvae lived to reach the fifth stage, but these were then all parasitised by the fly.

Final proof that *Ptychomyia* would live in Fiji quite independently of *Levuana* was obtained from the small island of Naigani, where neither cabbages nor raintrees occur. The last outbreak of *Levuana* had finished in March 1926, and in October Tothill and Paine failed to find any " carry over " trees, in spite of cutting down the most likely ones. Visits were made again in November of the same year and in April, June and August of 1927, with similar results. On the occasion of the last-mentioned visit, when it was extremely probable that *Levuana* had been absent from the island for a year, some *Levuana* larvae were introduced. Thirty-two of these lived to be either fifth-stage larvae or pupae, and of these no less than twenty-seven were parasitised by *Ptychomyia*.

This evidence, together with more of the same kind, indicated to our satisfaction that effective, if unknown, secondary hosts were present in the bush and that *Ptychomyia* could live in Fiji independently of *L. iridescens*. The Committee was therefore relieved of the necessity of having either to increase the supply of cabbages and raintrees or to introduce a bush-feeding Zygaenid from New Guinea.

Conditions on Makuluva.—Before speaking of the general position at the end of 1928, reference may be made to the small island of Makuluva. This low coral islet near the mouth of the Rewa River is perhaps a half-mile from Nukulau to windward from it and much exposed from its location on the edge of the reef. Its soil, only a few feet in depth, is composed for the most part of comminuted shells, its arboreal flora is limited to a relatively few examples of perhaps five species of ordinary beach trees and a large number of coconut palms. The insect fauna is extremely meagre, but, in spite of its exposed location, *Levuana* was able to establish itself on the coconut trees there, and there, too, *Ptychomyia* succeeded in finding it without human assistance, having spread probably from Laucala point on the mainland with an intermediate generation on Nukulau. It is an interesting, and to us significant, fact that whereas *Levuana* had diminished very rapidly in numbers within six months of the introduction of *Ptychomyia* in almost every part of its known range in Fiji, it continued to persist in considerable numbers on Makuluva for the three following years.

An outbreak started in October 1925, but as the island is exposed to the full force of the trade winds, it was confined chiefly to the leeward side. By March 1926, *Ptychomyia* had achieved a parasitism of approximately 80 per cent., and overlapping of broods was the rule. By November 1926 the outbreak had increased so that even the windward trees were attacked, but the parasitism had now dropped to 45 per cent. and the overlapping of broods had lessened to the extent that neither fourth and fifth-stage larvae nor pupae were represented. In January 1927 the moth was still active everywhere, and the stages were further restricted so that only second to fifth-stage larvae were present. In June 1927 the outbreak had become reduced in severity, but *Levuana* was still abundant chiefly as second-stage larvae, the parasitism in the last brood of pupae having risen to 65 per cent. In September 1927 conditions were very similar as to abundance of *Levuana*. There were then a few fifth-stage larvae, many pupae, swarms of moths, numerous eggs and a few first-stage larvae, but the parasitism had become reduced to 19 per cent.

On October 6th the insect was still abundant enough to enable a collection of 2,000 larvae to be made from four leaves. Practically all were in the first to third stages, and most of the third-stage larvae were parasitised. On November 1st, 1927, there were a few fourth-stage larvae, numerous fifth-stage larvae, masses of pupae, a few moths and an occasional egg-mass. The parasitism of fresh pupae in 200 examined had fallen to the new low level of 2·5 per cent. *Levuana* thus had a new lease of life and by December 1927 was again present in swarms, the parasitism having increased to 10 per cent. by the same date. The increase of *Levuana* went on until January 1928, when there was a sudden sweeping destruction of *Levuana* due to pupae being massed together and the moths being unable to emerge therefrom. In March 1928 the moth was extremely scarce, and there was a high percentage of *Ptychomyia* parasitism in recent pupae. Three weeks later, only 100 larvae could be found, chiefly in the fourth and fifth stages, and on these the parasitism was heavy. No examination has been made since, but the record given above shows that *Ptychomyia* is relatively impotent in the control of *Levuana* when secondary hosts are absent.

The General Position in January 1929.—As this report is being written, there has been no new outbreak of *L. iridescens* for three years, and the insect has become so rare that a visiting entomologist searching specially for it would almost certainly be disappointed unless directed to one or two trees in the Rewa delta where there are few secondary hosts and where the moth has been carrying on an erratic and, so far, indeterminate struggle with *Ptychomyia* for the past few years. It is much less abundant than is *Artona* in Malay and Java, and the anticipated small outbreaks have so far failed to develop ; in fact, the only places so far as we know where *Levuana* has been able to survive at all are on islands like Makuluva and in the Rewa delta where secondary hosts appear to be equally scarce.

Economic Value of the Campaign.—The Citrus Industry of California was saved from the ravages of the Cottony Cushion Scale by the introduction of a lady beetle from Australia ; the sugar-cane industry of Hawaii was saved from disaster by the introduction of a Tachinid fly from Java that attacked the cane borer ; and it appears to be no less certain that the copra industry of Fiji has been extricated from an awkward predicament by the introduction of *Ptychomyia.* The threat of disaster overhanging Vanua Levu, Taveuni and Lau has been removed ; Ovalau and nearby islands are now producing their normal 500 tons of copra, and, what appears to be of greater importance, the hitherto non-productive island of Viti Levu, which is about the size of Jamaica, is now producing copra, and the natives have commenced to plant up actively in a campaign energised by the Secretary for Native Affairs.

We are inclined to think that the most important result of the campaign is the one least capable of measurement, namely, that coconuts can now be grown on Viti Levu. Within a decade the premier industry of the Colony, namely, the manufacture of raw sugar was threatened with financial failure, a threat which brought home the convincing fact that there was no other crop to replace sugar cane in case of its forced withdrawal. The seriousness of the position convinced the Government of the day that it would be prudent to diversify the agriculture of the Colony—its only source of wealth—and it has since moved in this direction by endeavouring to establish cotton, pineapple canning, and dairying. It would still be a disaster if raw sugar were to be forced off the list of exports, but the position could be faced to-day in a way that would have been impossible in 1922, because we now know that every acre of land under cane could be converted into dairy farms or coconut plantations and that in the end the essential stability of the Colony would remain unimpaired.

Another result of the campaign, also not calculable in money terms, is that it helps to insure the prosperity of the native races of the South Pacific depending so largely upon the coconut palm. *Levuana* introduced without parasites to the Lau islands of Fiji, into Rotuma or into the Gilbert and Ellice group and into many other islands of Polynesia and Micronesia might have caused those islands gradually to become depopulated, and, as transportation by sea became more rapid and more frequent, such introductions might have occurred.

The difficulties caused, or likely to be caused, by the *Levuana* moth prior to its control were described in an article published in 1923 by Sir J. Maynard Hedstrom, a life-long resident of the Colony, who as Senior Member of the Legislative Council, as head of the firm of Morris, Hedstrom and Company, and as President of the Suva Chamber of Commerce, was singularly competent to deal with this subject. The difficulties that have been overcome are those mentioned in the article referred to, and I will quote briefly therefrom :

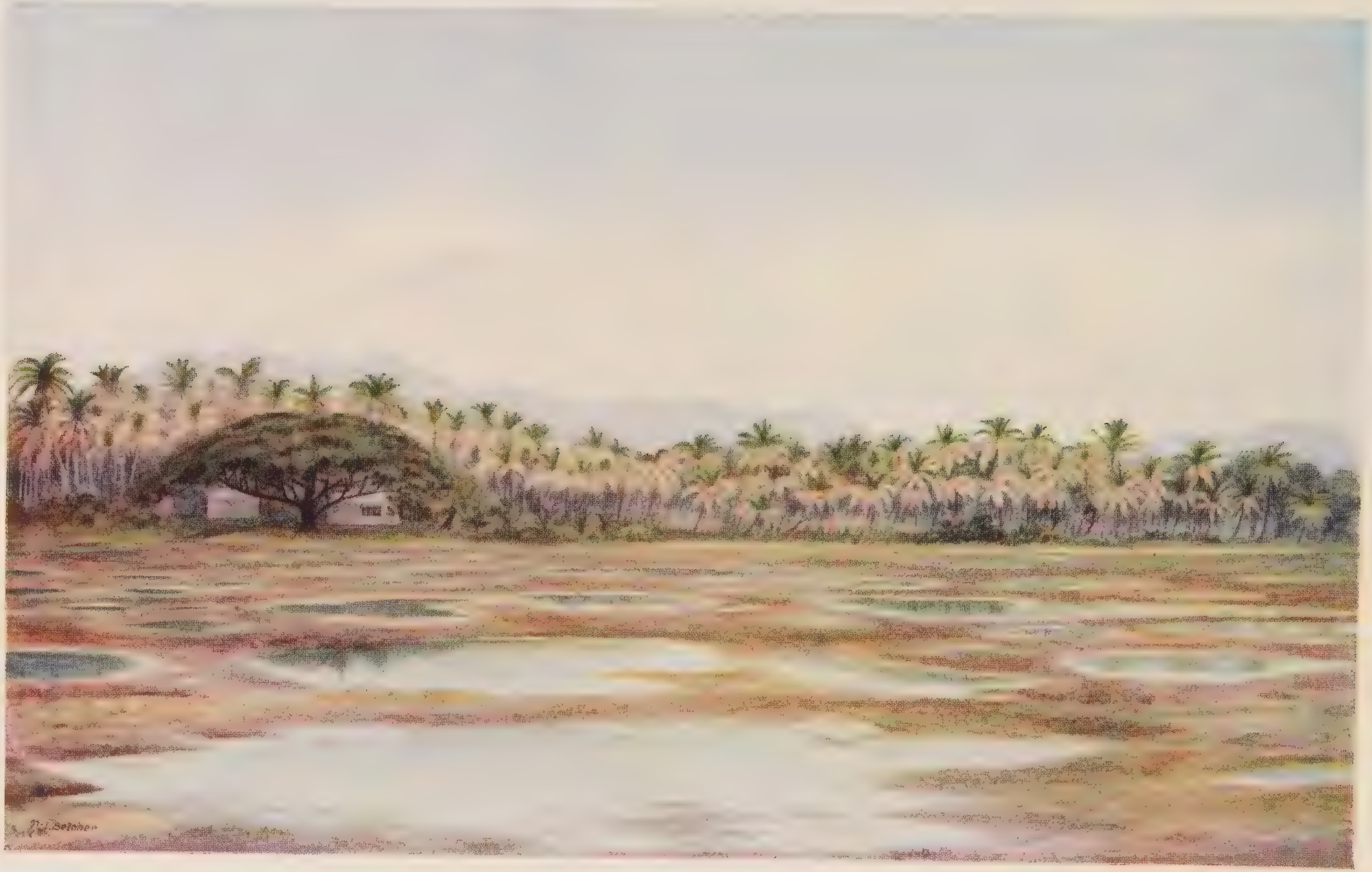
> " Any serious check to our sugar industry would have a disastrous effect on the Colony, particularly upon the Administration and the mercantile community, but, speaking broadly, it would not have a crushing effect on the native race, whereas the loss of the copra industry would utterly impoverish the natives of Vanua Levu, Taviuni, Lomaiviti, and Lau, and render conditions of life and Administration in those districts very difficult.
>
> " Owing to the central position of Ovalau and Moturiki, and the constant traffic from those islands to Vanua Levu, Taviuni and Lau, it would be unsafe to reckon on any definite period of immunity for the other coconut-bearing areas in the group.
>
> " The spread of *Levuana* to the islands of Lomai Viti, Vanua Levu, Taviuni and Lau would mean the disappearance of copra as an article of export, and the ruin of practically every copra planter. I wish to avoid exaggeration, but I believe observers who are familiar with the damage done by the *Levuana* moth on Viti Levu, and its more recent ravages on Moturiki, will agree that the above is not an over-statement."

PLATE II

THE RECOVERY OF COCONUT PALMS FOLLOWING UPON AN OUTBREAK OF *LEVUANA*

A typical scene on Ovalau in 1925 as viewed from the reef at low tide. The coconuts have been defoliated by *Levuana* larvae, the outbreak subsiding with the exhaustion of the food supply. The recovery is indicated by the presence of about eight green leaves per tree above the ash-coloured dead ones. The tallest trees are of the type referred to in the text as " carry over " trees because *Levuana* survived on them in small numbers between outbreaks.

PLATE II



AN ACCOUNT OF THE LEVUANA MOTH

SYSTEMATIC

Levuana iridescens is a Lepidopterous insect belonging to the family ZYGAENIDAE. This family contains four sub-families, the PHAUDINAE, HIMANTOPTERINAE, CHALCOSIINAE, and ZYGAENINAE. The genus *Levuana* has been placed by Jordan in the sub-family CHALCOSIINAE, and contains only the one species, *L. iridescens.*

The family ZYGAENIDAE is defined by Jordan in the following terms :—

> " First (anterior) sub-median vein in both wings developed. Forewing without areole. Frenulum and retinaculum are wanting in the HIMANTOPTERINAE. A more or less distinctly prominent vein in the cell of both wings developed from the base to the end of the cell. Costa of the hindwing mostly separated from the cell, running parallel with it and connected with it by a short oblique nervure, more rarely the costa coincident with the cell. Ocelli mostly present. Claws without tooth."

Many Zygaenids are very similar in general appearance to certain Syntomids, and others are morphologically similar in many respects to the PSYCHIDAE, LIMACODIDAE, and CASTNIIDAE. Moreover, many of the features included in Jordan's definition are shared by other families, but the ZYGAENIDAE may be recognised with certainty by the four following features, considered together :

1. Vein Cu_2 well developed in both wings and not connected with any other vein.
2. Both wings with M present within cell.
3. Hindwing with $Sc-R_1$ approximated to, but separate from, cell and connected with it by a bar (R_1).
4. Haustellum present (except in HIMANTOPTERINAE and PHAUDINAE).

Levuana exhibits all these characteristics.

The PHAUDINAE and HIMANTOPTERINAE are aberrant and highly specialised sub-families in which the mouth-parts are aborted, and ocelli are absent in most species. The HIMANTOPTERINAE are further characterised by the absence of retinaculum and frenulum and by prolongation of the hindwing to form a long, thin tail. None of these features is found in *Levuana.*

The CHALCOSIINAE and the ZYGAENINAE are much less specialised. The mouth-parts, ocelli, and retinaculum and frenulum are well developed in both of these sub-families. The only absolutely constant distinguishing feature is the presence or absence of spurs on the fore-tibiae. The CHALCOSIINAE are entirely without spurs on the fore-tibia. The ZYGAENINAE have one such spur. *L. iridescens* has no spur on the fore-tibia and is therefore allocated to the CHALCOSIINAE.

The CHALCOSIINAE are an essentially tropical group. Most of the species occur in the Indo-Malayan Region, and the occurrence of *L. iridescens* in Fiji is anomalous. The majority of CHALCOSIINAE are medium or large-sized moths, often brilliantly coloured and bearing striking resemblances to butterflies. On account of its small size and narrow wings *L. iridescens* differs in general appearance from most CHALCOSIINAE and is much more similar to the ZYGAENINAE. Further, in certain structural features (discussed in the next section) it shows a closer affinity to the ZYGAENINAE than to the CHALCOSIINAE, but until the ZYGAENINAE as a whole are more thoroughly understood we must adhere to Jordan's classification and place *Levuana* in the CHALCOSIINAE.

The genus *Levuana* was first described by Bethune-Baker in 1906 as follows :—

"Antennae bipectinated in both sexes. Palpi minute porrect. Mid and hind tibiae with minute spurs. Wings moderately broad, expanding in the primary slightly outwards. Neuration : cell very long to nearly three-quarters of the wing in both wings ; primaries, vein three given off from the angle, four and five about the angle, six and seven stalked from above the middle of the cell, eight given off from seven close to the termen, nine from the angle, ten midway between nine and eleven, eleven from beyond the centre of the cell ; secondaries, vein two from well in front of the angle, strongly bent downwards, three from the angle, four absent, five from the centre of the cell, seven absent, eight connected with the cell by a short bar. Type, *Levuana iridescens*, B.B."

The species *L. iridescens* was described by Bethune-Baker as follows :—

"*Male and Female.*—Head and thorax steel-blue ; abdomen and legs ochreous. Primaries deep unicolorous steely-blue without any markings ; secondaries, iridescent steely-blue, semi-hyaline, especially from vein 1 c. to vein 5."

Jordan gives the following description of the genus and the species :—

"Genus" : *LEVUANA*, Baker.

"Head long ; palpi thin. Antennae in the female pectinated only distally, simple proximally, beneath concave lengthwise. Wings narrow, forewing with 5 subcostals, the 1–3 free from the cell, the 4 and 5 stalked, the 1 radial from this stalk, the 2 and 3 radials and the 1 median from the lower angle of the cell ; in the hindwing the 1 and 3 radials absent.—Fiji.

"*L. iridescens*, Baker. Antenna, head, thorax, breast and upper surfaces of the forewing glossy green-blue ; abdomen, legs and tongue yellow. Hindwing semitransparent, above iridescent green-blue.—Viti-Levu."

Jordan's definition of the genus is incorrect in one particular. He says, "In the hindwing the 1 and 3 radials are absent." Actually, the 1 radial (*i.e.* M_1) is present, but stalked with Rs. The 3 radial (*i.e.* M_3) is completely fused with 1 median (*i.e.* Cu_{1a}).

RELATIONSHIPS AND PHYLOGENY

1. Characters Useful as Indications of Relationships

The classification of the Zygaenidae is a matter of considerable difficulty. The Phaudinae and Himantopterinae, which are small and highly specialised sub-families, have little in common with the more typical Zygaenids and are clearly far removed, phylogenetically, from them. Up to this point classification is a simple matter and the division is a natural one, but the separation of all the remaining Zygaenids into groups in a manner which will satisfy both the bionomist and the systematist is a very difficult problem.

The Zygaenidae, except the Phaudinae and Himantopterinae, are divided into two large sub-families, the Chalcosiinae and Zygaeninae, which are generally regarded as being clearly defined and widely separated from one another. Actually, however, the distinction is very slight, and in many cases the division does not appear to be a natural one. It is certainly possible, for each of these sub-families, to prepare a list of characters which are shared by many genera in that sub-family, and not by many of the other sub-family, but the exceptions are so numerous and the connecting links so complete that many features which appear at first sight to separate the two sub-families satisfactorily prove to be nothing more than matters of degree. The characters cited by Jordan as typical of Chalcosiinae are :—

1. Tongue and palpi present.
2. Palpi often short, separated from eye by stripe on face which is usually scaled.
3. Stripe which surrounds eye at back broad, sometimes without scales, always with fine erect hairs.
4. Ocelli present.
5. Antennae in male and female pectinated and dentate at least before tip.
6. Fore-tibia without spur, middle and hind tibiae with one pair of short spurs.
7. Anal segment of female usually modified into ovipositor.

Of these seven characters, the only one which applies satisfactorily as a distinguishing feature to all members of this sub-family is the absence of a spur on the fore-tibia.

Similarly, in the case of the Zygaeninae, the only character which can be cited to separate all the species from the Chalcosiinae is the presence of a spur on the fore-tibia.

The separation of all the less specialised Zygaenidae into sub-families therefore depends solely on the presence or absence of spurs on the fore-tibiae, despite the very large number of species and the great assortment of forms involved, and regardless of the characters of the larvae and pupae. This basis of classification seems arbitrary, insufficient, and unnatural. The discrepancy is emphasised here because *Levuana iridescens* is one of those species that seems to be misplaced in the scheme of classification.

In the course of our search in Malay, Java and New Guinea for parasites to attack *Levuana* in Fiji, several Zygaenids which showed resemblances to *Levuana* in all their stages were selected in the field for special study in the belief that they would be the most likely species to yield parasites that would attack *Levuana*. The bionomics of these were studied before their systematic position was determined, and the similarities between them and *Levuana* in all stages were found to be so great that it was taken for granted that they must be very nearly allied. But when a closer study of the adults was undertaken, it was found that they differed greatly from *Levuana* in their wing-venation and in that they all possessed long spurs on the fore-tibiae. These characters necessitated their being placed, not only in a different genus, but also in a different sub-family. They were, in fact, all members of the genus *Artona* in the sub-family ZYGAENINAE, and the most important of them were: *Artona catoxantha*, *A. trisignata* and *A. albicilia*. The larva of *A. catoxantha* is almost identical in size, structure, colour, habits and food-plants with that of *Levuana iridescens*, and a close examination would be necessary to distinguish them if they both occurred in the same place. The same applies to the cocoons, which are of a peculiar and very characteristic type. So far as general appearances are concerned, the adults of *A. catoxantha* differ from *L. iridescens* only in colour; their habits, including the characteristic resting attitude, are identical. The other two species of *Artona* show the same close resemblances in all stages, except that their larvae differ in colour and in their food-plants from *L. iridescens*. Yet, despite these apparently very close natural affinities, *Levuana*, on account of the lack of spurs on its fore-tibiae, is so widely separated from *Artona* in the scheme of classification as to be placed in another sub-family, to most of the other species of which it bears scarcely any resemblance.

Levuana possesses all the features enumerated above for the CHALCOSIINAE, but none of them, except No. 6, is peculiar to that sub-family. It is true that the palpi of *Artona*, for instance, are very slightly longer, relatively to the size of the face, than those of *Levuana*, and that they are situated nearer to the eyes; but the difference between the two genera in this respect is less than the difference between either one of them and others in its own sub-family. The stripe which borders the eye at the back is as broad in *Artona* as in *Levuana*. The antennae of *Artona* are different from those of *Levuana*, but they vary so much within each sub-family that they cannot be regarded as important distinguishing features. Mouth-parts and ocelli are well developed in *Artona* as well as in *Levuana*. It is therefore apparent that the only morphological features of the adults which can be of any assistance in determining the affinities between *Levuana* and other genera, notably *Artona*, are the wing-venation and the tibial spurs.

2. RELATIONSHIPS INDICATED BY TIBIAL SPURS

The fore-tibia of *Levuana* possesses no spurs at all, and there is no indication, either as a rudiment or a vestige, of the long spur which is so characteristic of the ZYGAENINAE. The middle tibia bears two very short terminal spurs which slightly overlap the first tarsal joint. The hind tibia possesses two terminal spurs identical with those of the middle tibia, and there is no trace of a median spur. This arrangement of the tibial spurs is remarkably constant throughout the CHALCOSIINAE with the single exception of the genus *Boradia*, which has no spurs on any of the tibiae.

The tibiae of *Artona catoxantha* are quite different. The fore-tibia bears one very long spur which arises near the proximal end of the tibia and extends just beyond its distal end. The middle tibia bears two short terminal spurs which are rather longer than those of *Levuana*. On the hind tibia there are two short terminal spurs, similar to those on the middle tibia, and also one longer median spur arising a short distance proximal to the middle point of the tibia. Another species of *Artona*, not yet identified, is identical in this respect with *A. catoxantha*. In *A. trisignata* the fore-tibia is the same as *A. catoxantha*, but the terminal spurs of the middle and hind tibia are smaller; the median spur of the hind tibia is often absent altogether, and when present, is always minute. The species *albicilia*, which is placed by Jordan in a separate genus (*Homophylotis*), has no median spurs on the hind tibiae, and the terminal spurs, both on the middle and hind tibiae, are very small. The spur on the fore-tibia, however, is well developed and is similar to that of typical species of *Artona*. Therefore the only essential difference, so far as the tibiae are concerned, between *Levuana iridescens* and these other species is that it possesses no spurs other than the terminal pairs, while *albicilia* has, in addition to these, one on the fore-tibia, and *A. catoxantha*, for instance, has one on the fore-tibia and one on the hind tibia.

In the sub-family ZYGAENINAE as a whole the number and distribution of the spurs on the fore and middle tibiae are constant (*i.e.* the same as *Artona*), but on the hind tibia they are very variable. There are two median spurs on the hind tibia in many species, one in several others, and often, as in *albicilia*, there are none at all. The terminal spurs on the hind tibiae are always present.

The family ZYGAENIDAE therefore contains almost all possible variations of the tibial spurs. If the total number of spurs on each tibia is expressed numerically, these variations can be illustrated by the following formulae :—

Typical ZYGAENINAE	1 : 2 : 4
Artona	1 : 2 : 3
A. albicilia	1 : 2 : 2
Levuana (CHALCOSIINAE in general)	1 : 2 : 2
Boradia	0 : 0 : 0

In this connection it is important to realise that the spur of the fore-tibia is not homologous with those on the other tibiae. It occurs in many families of Lepidoptera and is always thin and lamellate in form. It is supposed by some authors to be used for cleaning the antennae. The other spurs, both median and terminal, are sharp, stout spikes, more or less circular in cross-section. Hence, if the tibial appendages are to be used as criteria for determining natural relationships, the lamellate spur of the fore-tibia must be considered separately.

This spur, unlike the ordinary spurs, does not occur in any other order of insects, not even in the Trichoptera, and is also absent in the Homoneura, the most primitive Lepidoptera. It must, therefore, be regarded as a specialised feature. In the case of the CHALCOSIINAE (including *Levuana*), in which there is no trace of a spur on the fore-tibia, the question arises whether these insects have been evolved from forms which have never possessed this spur or from forms which were furnished, like *Artona*, with one such spur and which have gradually lost it. There is very little evidence with which to answer this question, but the little that is available indicates that the spur was formerly present. The peculiar and characteristic form of Zygaenid larvae, pupae, and cocoons, which is common to all species, indicates a fairly close relationship between CHALCOSIINAE and the ZYGAENINAE in general; and it is difficult to believe that the former sub-family, which includes such a great assortment of forms in every other respect, can have been derived from forms which always differed from the ancestors of ZYGAENINAE in this one particular. Moreover, the spur is present in those Zygaenids which, judging from the wing-venation, are the most primitive. It is, therefore, far more likely that the fore-tibial spur was formerly possessed by all species, and its absence in so many different species must be regarded as indicative of a tendency, prevalent throughout the family, for this spur to disappear. In the special case of *Levuana iridescens* and *Artona catoxantha*, which show such remarkable similarity in their early stages, we are forced to the conclusion that *Levuana* originated from a form resembling *Artona* as regards the fore-tibial appendage. The subsequent disappearance of this appendage in *Levuana* must be regarded as a decided secondary specialisation. It was thought possible, in view of this conclusion, that a vestige of this spur might be produced at some stage during the development of the pupa, but a close study of the leg rudiments in the pupa failed to reveal any such organ. However, although the discovery of it in the pupa would have strongly supported the conclusion just drawn, its absence does not disprove that conclusion.

The significance of the variation in number and distribution of the ordinary spurs in ZYGAENIDAE is more obvious. A comparison of the ordinary spurs of ZYGAENIDAE with those of the more primitive families of Lepidoptera shows that the possession of the full complement of spurs (*i.e.* two terminal on the middle leg, and two median and two terminal on the hind leg) is the most primitive condition. The various types of Zygaenids included in the foregoing list of formulae are arranged in descending order according to the number of spurs they possess, so that the first formulae (1 : 2 : 4) represents the most archaic condition of the spurs and the last (0 : 0 : 0) the most specialised. *Levuana*, with all typical CHALCOSIINAE, comes nearly at the bottom of the list, having no median spurs at all, and is, therefore, more specialised than ZYGAENINAE in general and *Artona* in particular. So far as the ordinary spurs are concerned, *Levuana* (0 : 2 : 2) is identical with *Artona albicilia* (1 : 2 : 2), and it is possible, within the sub-family ZYGAENINAE, to find almost all the connecting links between the 1 : 2 : 4 condition and the 0 : 2 : 2 condition. The terminal spurs show a gradual reduction in size, and the median spurs show a diminution in number and size. In typical species of *Artona* one median spur has completely disappeared; in others both have disappeared, as in *Levuana*. Therefore, in this respect also, *Levuana* exhibits marked specialisation as compared with most Zygaeninae, though some are specialised to the same extent.

3. Relationships indicated by Wing Venation

The wing-venation of Zygaenidae shows many different modifications, but there are four features that are common to all genera and to nearly all species. These are the presence of Cu$_2$ and M in both wings, the relation of Sc to R$_1$, and the complete absence of the areole. The vein Cu$_2$ is usually very well developed and shows no tendency to coalesce with any other vein. M is often well developed too, though in other cases it is often reduced to a mere vestige. The presence of these two veins is a distinctly archaic feature and contrasts strikingly with the specialisation indicated in other ways, notably the complete absence of the areole. This combination of primitive and specialised features is very characteristic of the Zygaenidae.

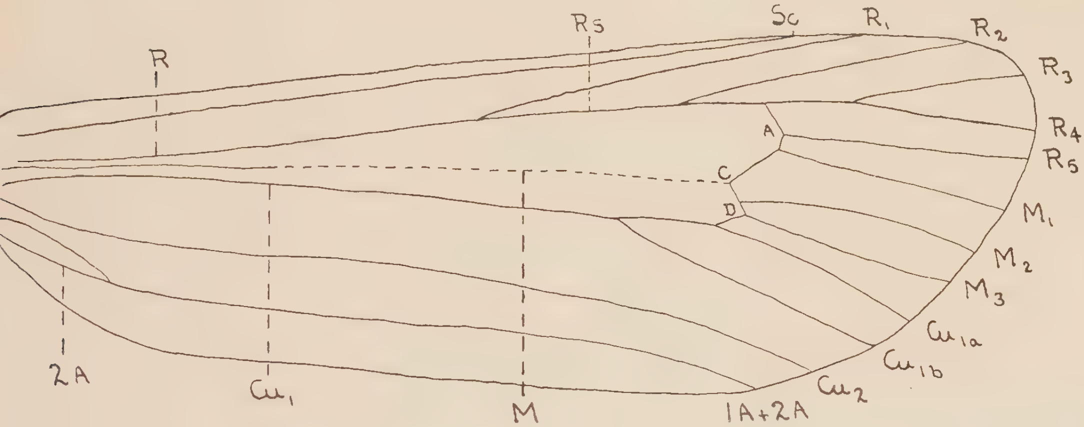


Fig. 1.—*Zygaena filipendulae*.—Forewing Venation.

The wing venation of *Levuana* (which is described on p. 119) exhibits several remarkable features, chiefly as regards the condition of vein M and its branches in both wings, the condition of the anal veins in the forewings, and the general shape of the cell in the hindwings. In order to appreciate the significance of these features it is necessary to consider the venation of a few other types of Zygaenidae also, firstly as regards the forewing and secondly the hindwing.

(*a*) **Forewing.**—The most generalised types of venation are found in the sub-family Zygaeninae. In the genus *Zygaena* (Fig. 1), for instance, all the radial and median veins of the forewing except R$_3$ and R$_4$ arise independently from the cell. The proximal portions of R_3 and R_4 have fused together, and the stalk R_{3+4} arises from the angle of the cell. R_5 arises from the cell, being connected with Rs by a cross-vein which forms part of the distal boundary line of the cell, but actually this cross-vein is the proximal end of R_5 which has become bent at an angle at the point A. This condition of R_3, R_4 and R_5 has resulted in R_5 arising from Rs at a point proximal to R_3. M_1 is well separated from R_5, but is more approximated to R_5 than to M_2. M_2 and M_3 are separate but are approximated at their points of origin. The cross-vein M_1–M_2 is bent inwards sharply at an angle at C. The main stem M extends independently and in a vestigial condition from the base of the wing across the cell to the point C. Cu_1 and its two branches are well developed, and Cu_{1a} is not specially approximated to M_3. Cu_2 is present and is far from Cu_1.

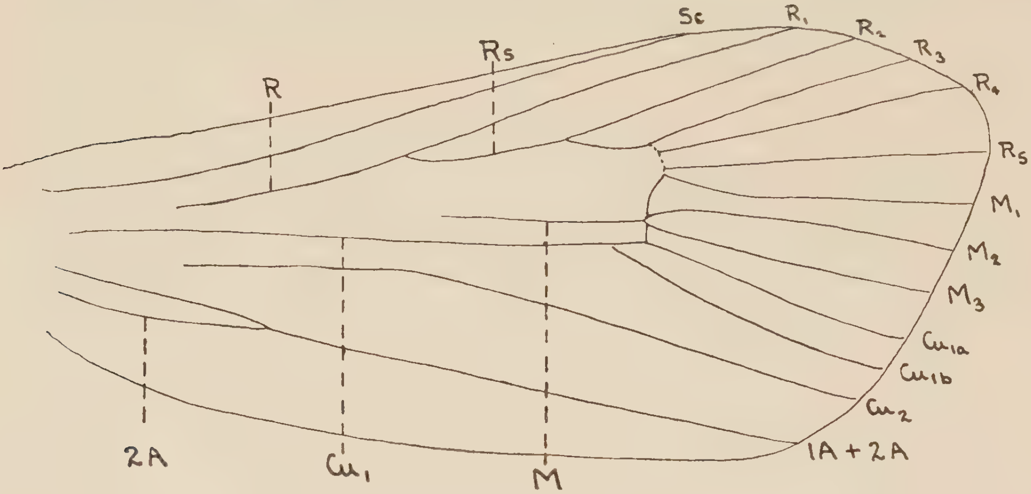


FIG. 2.—*Artona albicilia.*—Forewing Venation.

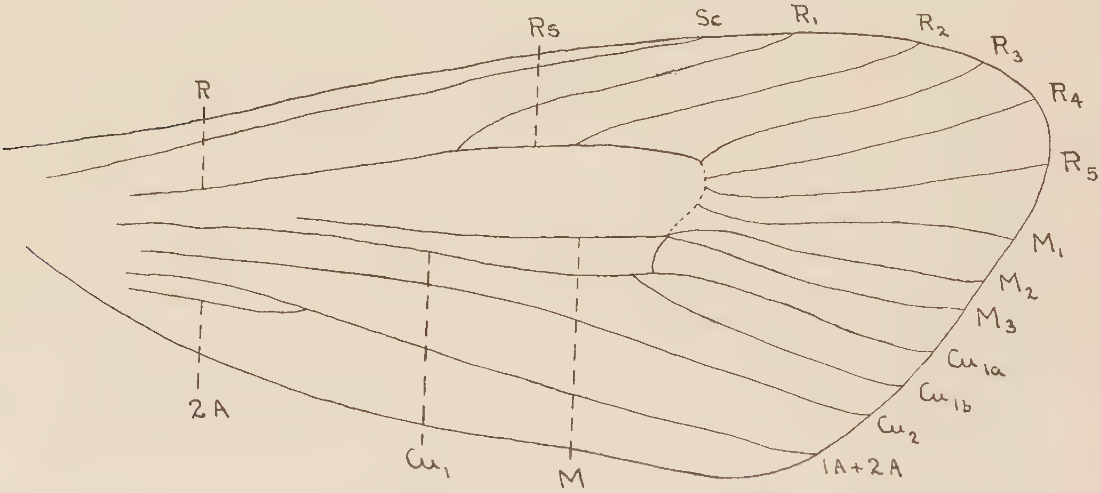


FIG. 3.—*Artona catoxantha.*—Forewing Venation.

2A forms a rather long loop at the proximal end of 1A, but otherwise these two veins are completely fused.

The forewing of the genus *Artona* (Figs. 2, 3 and 4) differs considerably from that of *Zygaena*. All the radial veins arise from the cell, a condition which is more primitive than that of *Zygaena*. The median veins arise from the cell also, but there is a tendency for M_1 to approximate to R_5, and for M_2 and M_3 to coalesce. The approximation of M_1 to R_5 is very apparent in *A. albicilia* (Fig. 2), more so than in *A. catoxantha* (Fig. 3) or in *A. trisignata* (Figs. 4A and 4B). M_2 and M_3 arise from the same point on the margin of the cell in *A. catoxantha* and *A. albicilia*. In *A. trisignata* they arise from two

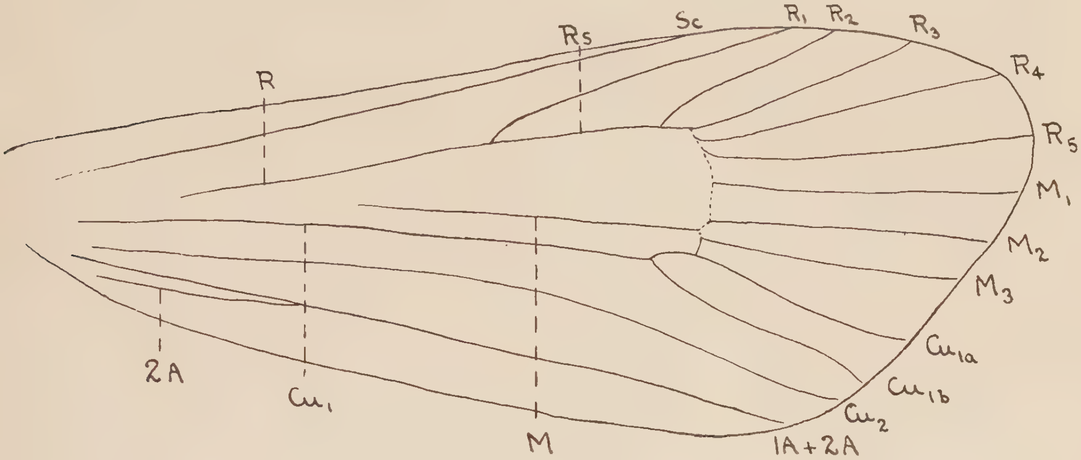

Sc
R1
R2
R3
Rs
R
R4
R5
M1
M2
M3
Cu1a
Cu1b
Cu2
2A
Cu1
M
1A+2A

FIG. 4A.—*Artona trisignata.*—Forewing Venation.

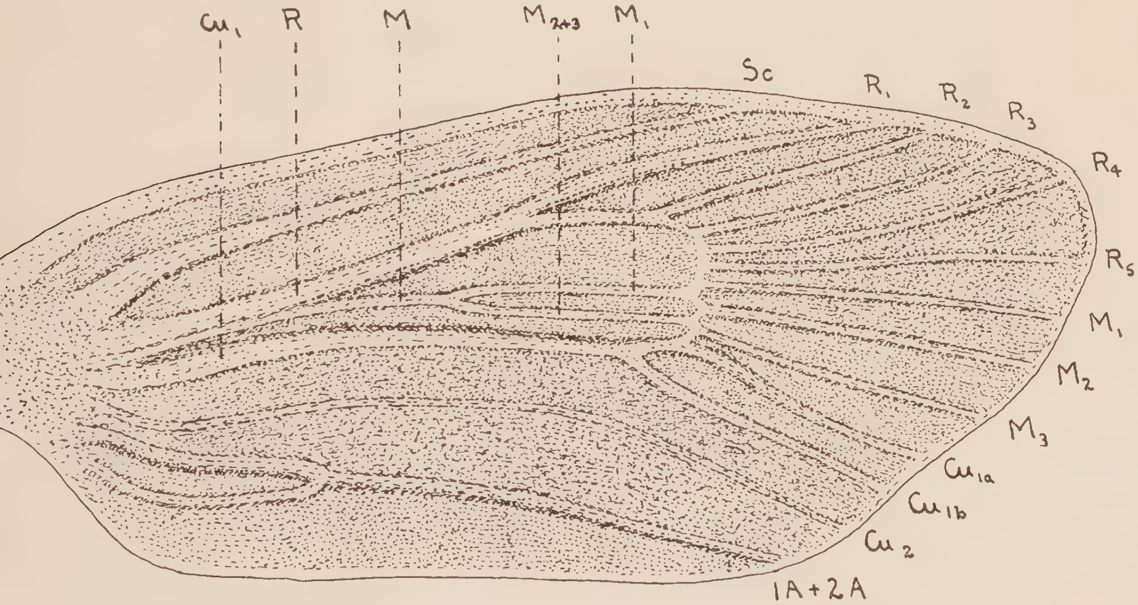

Cu1
R
M
M2+3
M1
Sc
R1
R2
R3
R4
R5
M1
M2
M3
Cu1a
Cu1b
Cu2
1A+2A

FIG. 4B.—*Artona trisignata.*—Pupal Forewing after Chitinisation of Veins. × 50.

separate but closely adjacent points. Vein M is present in all three species but is very faint and vestigial. In the basal region of the wing it has atrophied completely, but it is usually apparent at about a third of the length of the cell from the base. From this point it extends parallel to Cu_1, and close to it, to the point of origin of M_2 and M_3. It is usually so little chitinised as to be scarcely visible, and in *A. albicilia* it is sometimes absent altogether. Cu_2 is always well developed except proximally. 2A forms a long loop with 1A at the proximal end of the wing in all species. The series of cross-veins which close the wings distally form an almost straight line in *Artona*, and are very faint, with the exception of the cross-vein M_3–Cu_{1a}, which represents M_4.

A comparison of the venation of *Artona* with that of a form like *Zygaena* shows a decided specialisation in *Artona*, except as regards the radial veins. The most important feature is the condition of vein M and its branches. M_1 tends to fuse with R_5 and M_2 with M_3. The series of cross-veins which close the cell distally are vestigial only. M has become approximated to Cu_1, so that the points C and D (in Fig. 1) have, as it were, coalesced at the point of origin of M_2 and M_3. This has had the effect of straightening the outer margin of the cell. A continuation of this straightening process has produced a rounded end to the cell which is slightly apparent in *A. trisignata* and more so in other genera of Zygaeninae (*e.g. Lophosoma*). The condition in which all the veins arise from the cell, as in *Artona*, is of common occurrence in this sub-family, and the result of the tendency for M_1 to fuse with R_5 is exemplified in several genera (*e.g. Ephemeroidea* and *Chalcosiopsis*) in which M_1 and R_5 are stalked together.

Before considering *Levuana*, it is necessary to understand more clearly the condition of the median veins in *Artona*. A study of the pupal wing (Fig. 4B) shows that the trachea M is very well developed and that near the base of the cell it divides into two branches, as in most primitive Lepidoptera. The two branches then extend, parallel to one another and to Cu_1, to the end of the cell, where the posterior branch divides into M_2 and M_3 and the anterior branch continues to the margin without dividing as M_1. In the adult the anterior branch has atrophied completely within the cell. The median vein which is present within the cell is the posterior branch only. This applies to all species of *Artona* (including *Homophylotis*).

The forewing venation of *Levuana* (Fig. 58, p. 119) differs markedly from that of *Artona* and *Zygaena*. The chief differences in the radials are that R_2 and R_3 show a tendency to coalesce and the proximal halves of R_4 and R_5 are fused together. The differences in the case of the median veins are very striking. M_1 has fused with R_4 and R_5 for a very short distance. The vein M, which is fused with R as far as the point Q and is atrophied completely beyond Q in most specimens, presents an almost unique condition. By examining the trachea of the wing rudiments in the pupa (Fig. 60), this remarkable modification of M can be followed in its earlier condition. The trachea M runs alongside R as far as Q and then turns away from R and crosses the cell to the point T where it divides into the two branches TP and TV. In most individuals TP and TV are nearly equal in length, but in many TV is much longer than

TP, and it is never shorter. Sometimes T almost coincides with P. This variation indicates that M is tending to shift towards Rs, lengthening TV and shortening TP until T and P coincide completely. This has the effect of straightening out the cross-vein which closes the cell distally, and it produces a result similar to that which is found in *Artona*. But whereas in *Artona* this result has been produced by a backward movement of M, in *Levuana* it has been produced by a forward movement of M. Further, in *Artona* the first branching of M occurs near the base of the cell, while in *Levuana* it occurs near the distal end of the cell (at T).

The cross-vein PTV ($=M_1M_2$) is never chitinised, and is always very faint. The trachea M persists in the adult as far as Q as a chitinised vein partially fused with R, but atrophies between Q and P or Q and T, as the case may be, except in very rare individuals (Fig. 59), in which its former position is marked by a faint but definite chitinisation between Q and P and a short distance from vein Rs.

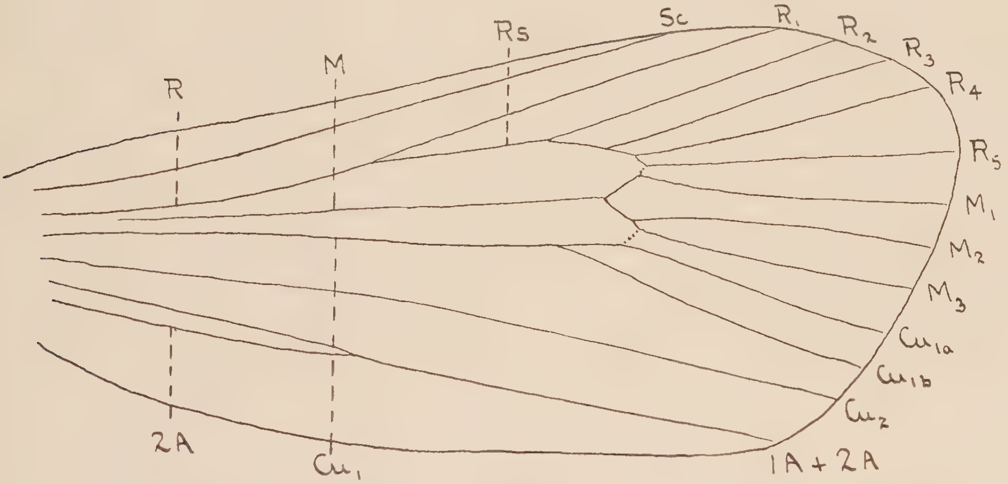


FIG. 5.—Suggested Forewing Venation of Common Ancestor of *Artona*-like and *Levuana*-like Zygaenids.

The only other highly specialised feature occurring in the forewing of *Levuana* is the almost complete fusion of 1A and 2A. This is a distinct advance on the condition found in *Artona*, for example.

These specialisations do not occur together in any other Zygaenid, although almost all other variations which are possible within one family are found. The variations in each sub-family are of a similar nature, and consist chiefly in the extent of coalescence of R_3, R_4, R_5 and M_1, and that of M_2, M_3 and Cu_{1a}. Neither sub-family possesses any special feature in its venation which can be considered characteristic of it, and nearly all genera of both sub-families show a curious combination of archaic and specialised features. Consequently, it is impossible to say that either sub-family is the more specialised, as far as the wing venation is concerned. In the case of the genera, however, it is possible in some instances to decide which is the more specialised, and this applies to the three genera which we are considering.

The greater specialisation of *Artona* as compared with *Zygaena* has already been pointed out. It is clear also that *Levuana* is more specialised than *Artona*, notably in the coalescence of M_1 and R_4 and R_5, the atrophy of M, and the disappearance of the basal loop on 1A+2A. But the modifications of M are entirely different, and in a sense opposed, in *Levuana* and *Artona*, and therefore *Levuana* cannot be derived from a form resembling *Artona* although either might be derived from a form similar to *Zygaena*, except as regards the radial veins. It is, in fact, possible, by comparing the archaic features of *Levuana* and *Artona*, to obtain a fairly clear idea of the ancestral form from which the two genera have deviated in different directions. Their common ancestor (Fig. 5) must have had all its veins, including Cu_2, and the main stem M, well developed. The radial veins were in a condition similar to that which still persists in *Artona*, and unlike that which is found in *Zygaena*. M divided the cell longitudinally into two nearly equal parts and joined the cross-vein which closed the cell distally near its middle point. The cross-vein was bent inwards. M_1 and M_2 were approximated to, but not coalesced with, R_5 and M_3 respectively, and 2A was partially fused with 1A.

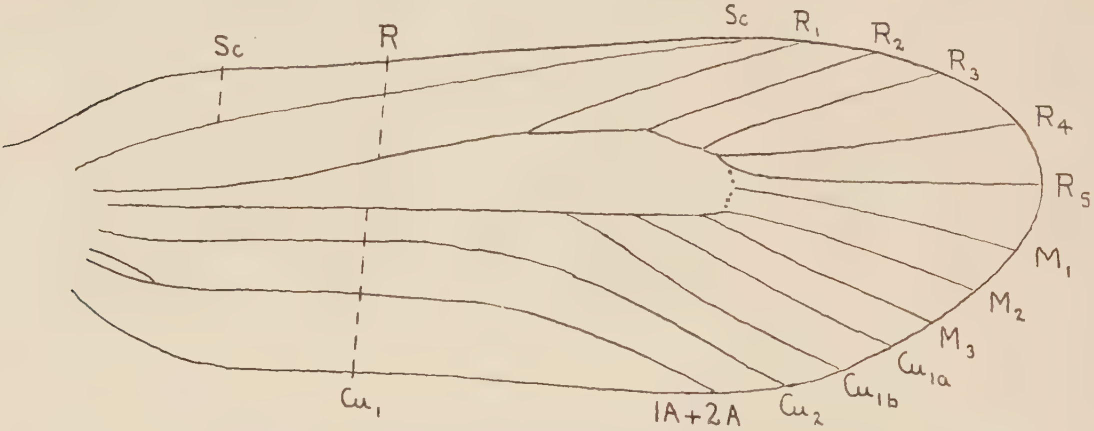


Fig. 6.—Zygaenid Y.—Venation of Late Pupal Forewing.

(*b*) **Hindwing.**—Turning now to the hindwings, we may again consider *Zygaena* as one of the more primitive types (Fig. 7). Cu_2 and two anal veins are well developed. All the other veins arise from the cell. Sc and R separate and extend side by side up to a point near the middle of the costal margin. R_1 is given off from this point and completely fuses with Sc for the rest of its length, the only free part of R_1 being the very short cross-vein between Sc and R. R and Rs form the anterior boundary of the cell, and Rs continues to the wing margin without branching. Three median veins are present: they and Cu_{1a} and Cu_{1b} form a series of almost equidistant and parallel veins between the cell and the wing margin. M runs across the centre of the cell in a vestigial condition and joins the distal margin of the cell between M_1 and M_2.

The hindwing venation of *Artona* is nearly the same in all species, and, as in the case of the forewing, shows considerable specialisation as compared with *Zygaena*. The relation between R and Sc is the same as in *Zygaena*, but R is atrophied proximally, and in *Artona albicilia* (Fig. 8) R_1 is so minute that R and Rs have almost coalesced with Sc at the point of origin of R_1. The part of Rs which borders the cell is vestigial, but from the cell outwards it is well developed. M_1 has atrophied completely except in a few individuals of *A. albicilia* in which it is present as a vestige between Rs and M_2. The main stem M is present as a faint vein in the distal part of the cell only and is much closer to the posterior border of the cell than the anterior. M_2 is continuous with M. M_3 has coalesced with Cu_{1a} for a short distance. A connecting vein joins M to M_3+Cu_{1a} in *A. trisignata* (Fig. 9) and *A. albicilia*, but in

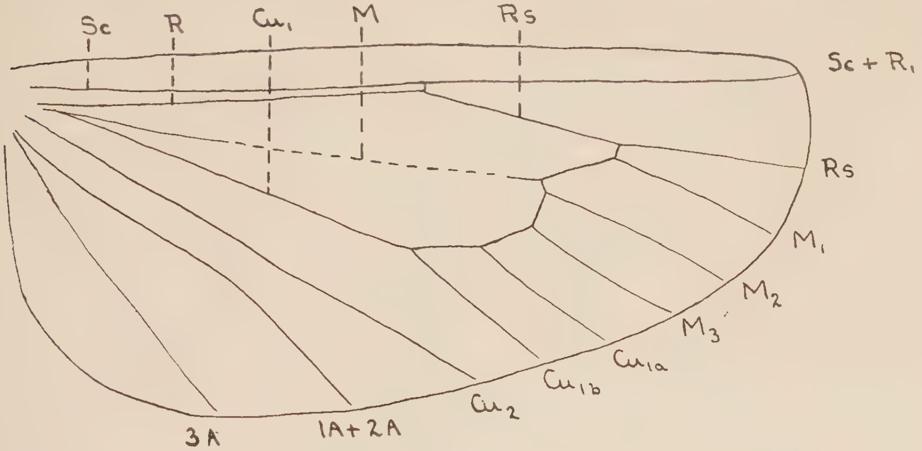


FIG. 7.—*Zygaena filipendulae*.—Hindwing Venation.

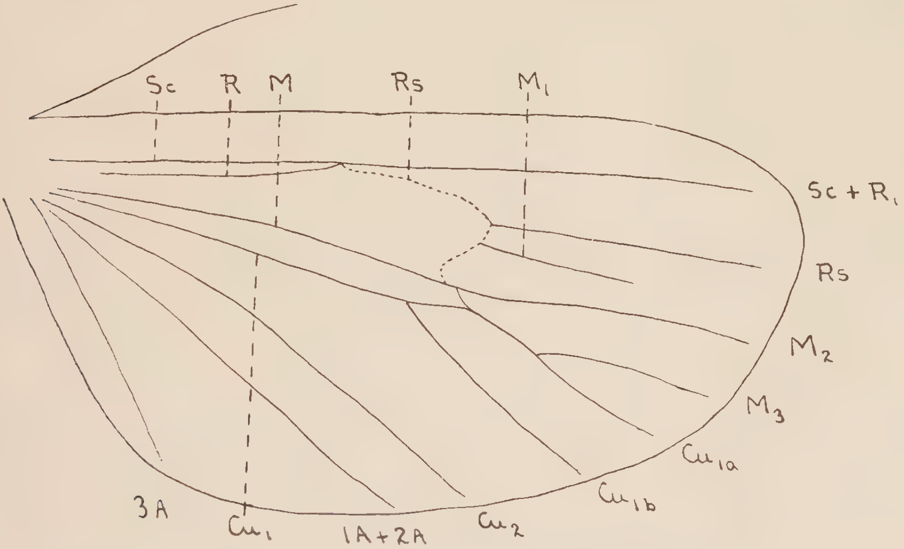


FIG. 8.—*Artona albicilia*.—Hindwing Venation.

A. catoxantha (Fig. 10) this cross-vein is obliterated by the coalescence of the distal end of M and the proximal end of M_2 with M_3+Cu_{1a} for a short distance.

The hindwing in the genus *Artona* is therefore greatly specialised as compared with *Zygaena*. There is a tendency for M_2, M_3 and Cu_{1a} to coalesce, and this tendency is associated with an approximation of M to Cu_1. M_1 atrophies.

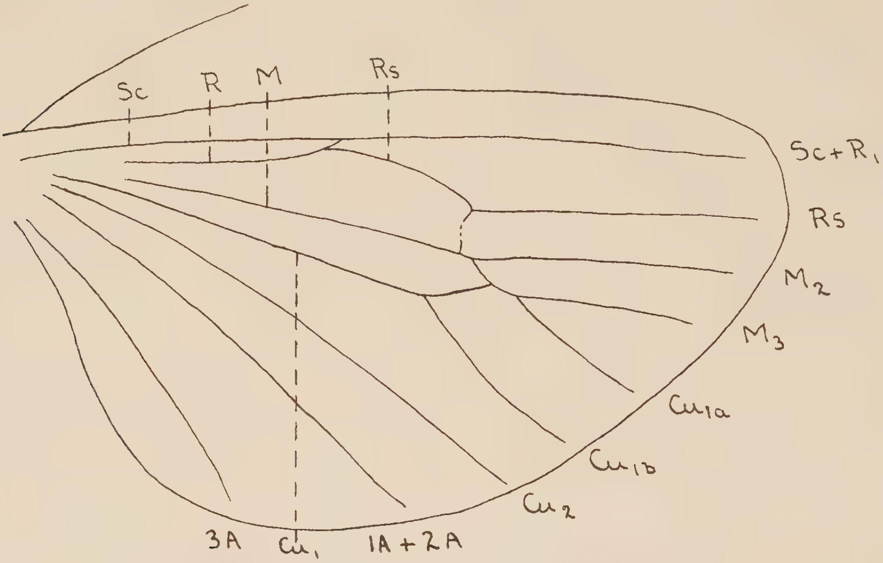

Sc
R
M
Rs
Sc+R₁
Rs
M₂
M₃
Cu₁a
Cu₁b
Cu₂
3A
Cu₁
1A+2A

Fig. 9.—*Artona trisignata*.—Hindwing Venation.

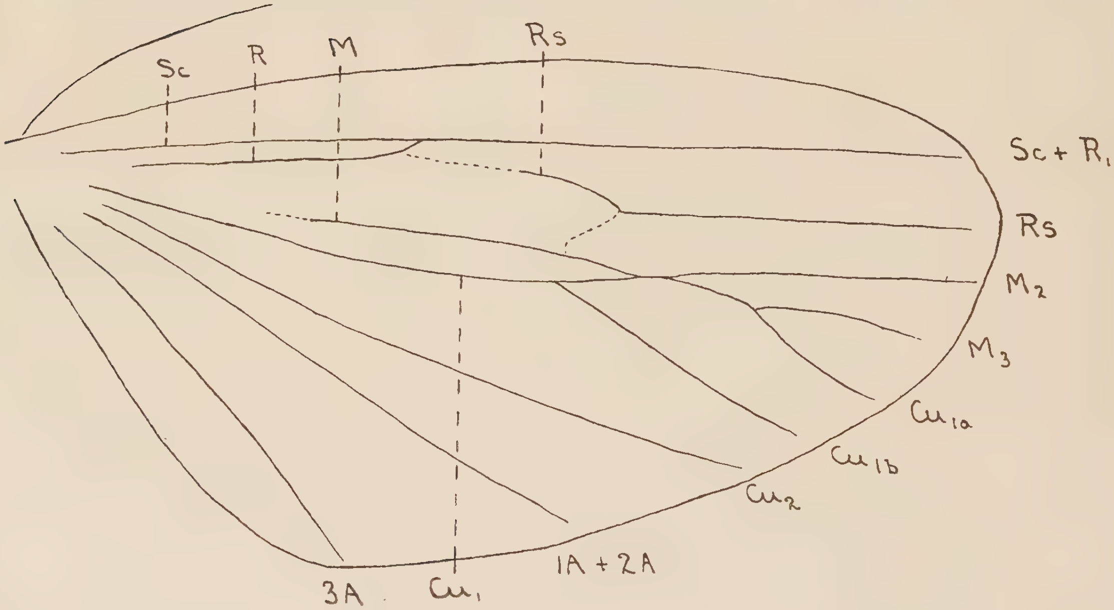

Sc
R
M
Rs
Sc+R₁
Rs
M₂
M₃
Cu₁a
Cu₁b
Cu₂
1A+2A
3A
Cu₁

Fig. 10.—*Artona catoxantha*.—Hindwing Venation.

The most obvious difference between the hindwings of *Levuana* (Fig. 61) and *Artona* are that the distal end of the cell is narrow and more or less pointed in *Levuana* instead of projecting inwards, that there is one vein less, that M is absent in the cell, and that apparently Cu_{1a} has not coalesced with any other vein. The means by which this unique condition has been derived can only be explained by reference to the trachea or the wing of the pupa (Fig. 63, p. 125).

The trachea Sc which precedes the vein Sc extends right along the wing near the costal margin. R runs along just behind it and parallel to it, and divides into two branches, R_1 and Rs. R_1 extends along beside the distal half of Sc, and Rs curves away from Sc. Immediately behind R and Rs, and closely approximated to them, is another trachea. This is M, and some distance beyond the point or origin of R_1, M divides into two branches. Of these, the more anterior (which proves to be M_1) continues alongside Rs for a short distance and then turns away from it, while the other (which is M_2) diverges widely from Rs before turning towards the margin of the wing. All these tracheae are clearly visible in a suitably stained wing-rudiment. There is no connection between M_2 and Cu_{1a} in the pupal wing. The adult venation is formed from these tracheae by the joint chitinisation of R and Rs with M to form one vein, and a similar fusion of Sc and R_1, and of Rs and M_1.

It is now clear that the hindwing venation of *Levuana* has been evolved from a primitive type, similar to that still found in *Zygaena* by the general coalescence of all the veins in the anterior half of the wing. R and Rs became approximated to M so that the distal half of Rs coincided and partly fused with M_1. In this way a narrow cell, without any trace of M extending across it, was produced, and the distal border of the cell became, as it were, bent outwards instead of inwards. The specialisation of the hindwing is, therefore, of the same nature as that of the forewing, notably as regards the shifting of M towards the anterior border of the cell.

This comparison of the hindwings of *Zygaena*, *Artona* and *Levuana* shows that *Artona* and *Levuana* have both been derived from a type similar to *Zygaena*, and that they have specialised in two entirely different directions; so that although *Levuana* is more specialised than *Artona*, the latter is not an intermediate form between *Zygaena* and *Levuana*. The hindwings therefore indicate the same relationship between *Artona* and *Levuana* as the forewings.

4. Relationship with a Zygaenid from the Solomon Islands

A search for *Levuana*-like larvae has been made in Malaya, Java, New Guinea, the Bismarck Archipelago, and the Solomon Islands, and nine different species have been discovered. The adults resulting from these, however, have all proved to be *Artona* (or *Homophylotis*) spp. with one single exception. This exception, which we call Zygaenid Y, was found in the Solomon Islands, and is of great interest when compared with *Levuana*. A number of larvae were found feeding on banana, and two of these duly pupated. In the meantime it was necessary for the work in the Solomons to be brought to an end, and the pupae of this Zygaenid had to be shipped to Sydney. Unfortunately the adults never emerged, although both of them were absolutely mature within the pupae, but by removing the cuticle of each pupa the adult was exposed and a fairly clear idea of its colour, venation, and arrangement of tibial spurs was obtained.

The colour of this species is as follows: Wings very dark, grey-brown, almost black, with a blueish sheen and no markings. Antennae, upperside of thorax, and tip of abdomen same colour as wings. Remainder of abdomen yellow. Underside, including head, yellow. Legs yellow, except distal halves of tarsi, which are dark.

The adult must bear a close general resemblance to *Levuana* in size and appearance.

The tibial spurs are 0 : 2 : 2, as in *Levuana*, and this fact places the insect in the CHALCOSIINAE.

The wing-venation is of great interest. The veins show well in the mature pupal wings. The preceding trachea had unfortunately atrophied completely before the pupae died. The pupal wings are shown diagrammatically in Figs. 6 and 11.

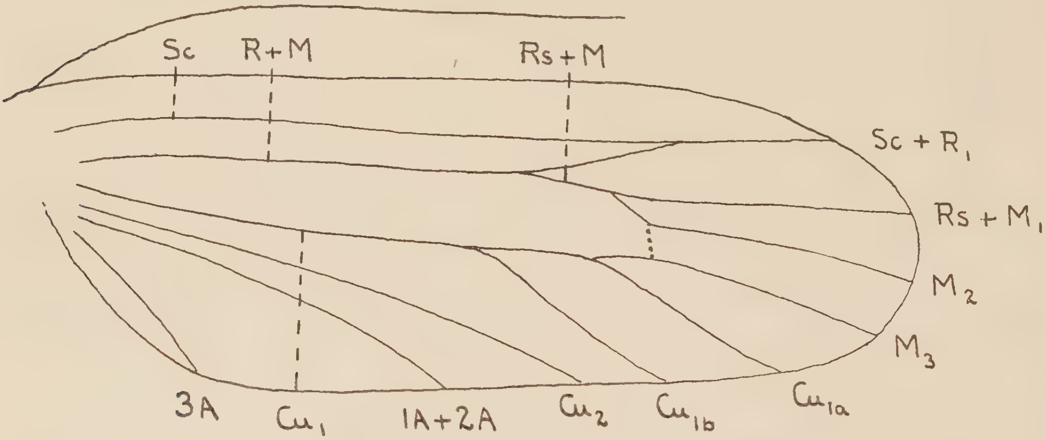


FIG. 11.—*Zygaenid Y.*—Venation of Late Pupal Hindwing.

The cell in both wings is elongated and more or less rounded distally, and all the veins in both wings arise from the cell. There is no trace of M in the cell in either. In the forewing all the veins are present. M_2 is slightly approximated to R_5, and M_2 to M_3. The cross-vein which closes the cell is not bent inwards. Cu_{1a} and Cu_{1b} arise from Cu_1 some distance proximal to the end of the cell. 2A forms a short loop at the base of 1A, the loop being shorter than in *Artona* and longer than in *Levuana*. The venation of the hindwing is peculiar, notably as regards the outward displacement, as it were, of the free part of R_1.* M_1 has fused completely with Rs. M_2, throughout its length, is nearly midway between $Rs + M_1$ and M_3. As in the forewing, Cu_{1a} and Cu_{1b} arise from Cu_1 some distance proximal to the end of the cell. M_3 is not approximated to Cu_{1a}.

* It is possible, but unlikely, that this is not R_1 but Rs which has fused distally with Sc, R_1 having atrophied. If so, the next vein is M_1, instead of $Rs + M_1$. This point cannot be decided definitely until early pupal wings, showing the tracheae, are available.

We have to decide whether this insect is more closely allied to *Artona* than to *Levuana*, or vice versa, or whether it is not specially related to either. In general appearance the forewing venation is similar to *Artona*, while that of the hindwing is more similar to *Levuana*. A close consideration, however, will show that in both wings the resemblance to *Levuana* is much greater than to *Artona*. In fact, there are only two respects in which Zygaenid Y resembles *Artona* as compared with *Levuana*. These are :

1. All the veins of the forewing arise from the cell.
2. There is no sudden narrowing of the vein R in the forewing, corresponding to that which occurs at Q in *Levuana*.

On the other hand, Zygaenid Y resembles *Levuana* as compared with *Artona* in the following important respects.

1. There is no trace of M in the cell of either wing.
2. The general shape of the cell in both wings.
3. The points of origin of Cu_{1_a} and Cu_{1_b} relative to the end of the cell.
4. The almost complete fusion of 1A and 2A in the forewing.
5. The fusion of Rs and M_1 in the hindwing.
6. The point of origin of M_2 from the cell in the hindwing.

It is not sufficient to show only that the resemblance between Zygaenid Y and *Levuana* are greater in number than those between Zygaenid Y and *Artona*. The relative significance of the resemblances must also be considered.

The fact that Zygaenid Y resembles *Artona* in that all the veins arise from the cell, while in *Levuana* R_4 and R_5 are stalked, is of no importance, since differences of this nature often occur between species of the same genus. The lack of a sudden narrowing of R in the forewing is, however, of great importance. It is clear, from what has been said concerning the relation of M to R in *Levuana*, that the uniform thickness of R in Zygaenid Y means either that the trachea M extends independently across the centre of the cell and atrophies without being replaced by a vein, or else that the trachea M coincides completely with R and Rs or with Cu_1. This last possibility concerning Cu_1 can be eliminated only by stating that there is no indication of fusion between M and Cu_1 ever occurring in ZYGAENIDAE and by considering the relationships between Zygaenid Y and *Levuana* indicated by other characters, including those of the larvae. The possibility of M occurring in the cell in the pupal wing and atrophying later could easily be settled if wing rudiments showing the tracheae were available, but as this is not the case, we must attempt to settle it by comparing Zygaenid Y with other species in this respect. In all *Artona*-like Zygaenids, in which M persists in the adult, and even in those in which it partially atrophies in the adult, M is very conspicuous within the cell in all pupae, including those which are quite mature. Further, in *Levuana*, in which that part of M which crosses the cell in the pupa atrophies completely in the adult so that the cell is entirely devoid of veins like that of Zygaenid Y, the position of M as a non-chitinised vestige is very apparent right up to the time of emergence of the adult. Yet in Zygaenid Y pupae of the same age there is not the least indication of M in the cell, or at the distal or proximal ends of the cell, nor is there any narrowing of the anterior boundary of the cell. It is, therefore, very reasonable to assume that the trachea M runs alongside R and Rs for the whole of its length, in exactly the same way as in the hindwing of *Levuana*, and that M chitinises with R and Rs to form a single vein in the adult. This view is further supported by the lack of an inward bend in the terminal cross-vein. In those specimens of *Levuana* in which the free part of M is abnormally close to Rs the cross-vein is straight. If in Zygaenid Y, M runs alongside Rs right to the end of the cell one would be surprised to find the cross-vein bent sharply inwards. Actually the cross-vein is bent slightly outwards.

Hence, if these deductions are correct (and there is not the least evidence to the contrary), the remarkable specialisation of the forewing of *Levuana* as regards M is paralleled, and is carried even further in Zygaenid Y.

Exactly the same reasoning applies to the hindwing, and the conclusion is that the condition of M in the hindwing of Zygaenid Y is identical with that of *Levuana*.

There is further evidence in support of this. In the hindwing of *Levuana* the vein Cu_1 always has a double appearance although it is preceded by only one trachea. This is due to the fact that during the formation of the veins an additional linear chitinisation takes place all along the anterior side of Cu_1. In the forewing no such chitinisation occurs, and Cu_1 has the normal single appearance. This suggests that the extra chitinisation is associated with the coincidence of M with R, for in the hindwing of *Levuana*, M and R have fused completely, but in the forewing the fusion is not yet complete. Possibly it serves to maintain the normal rigidity of the wing when M disappears as such. In Zygaenid Y this extra chitinisation along the anterior of Cu_1 is very apparent in both wings, and in both wings it seems that M has fused completely with R. In *Artona* spp., in which M is present within the cell in both wings, this additional chitinisation never develops.

Zygaenid Y is evidently slightly more specialised than *Levuana* as regards the condition of M, the complete fusion of Rs and M_1 in the hindwing, and the outward displacement of R_1 in the hindwing. In one or two less important respects, such as the degree of fusion of 1A and 2A in the forewing, it is a little less specialised. The important point is, however, that Zygaenid Y is specialised in exactly the same general way as *Levuana* and in an entirely different way from *Artona*. It probably belongs to the genus *Leptozygaena*, of which only one adult is known. This adult came from New Guinea.

The relationships indicated by the larvae of *Levuana* and Zygaenid Y are discussed in the next sub-section.

5. Relationships Indicated by Larval Characters

It remains to be shown whether the relationships indicated by the adult characters are confirmed by a comparison of the larvae. We cannot here undertake a very detailed study of the larvae of *Artona*-like, *Levuana*-like species, but by tabulating their most important and characteristic features it is possible to form a general idea of the relationships between them.

The chief characters used in distinguishing the larvae of Zygaenid species are the presence or absence of the following :—

A. Fleshy anterior rim or flange to prothorax.
B. Lateral glands on prothorax.
C. Median dorsal papilla on prothorax.
D. Pigment on cervical shield.
E. Very prominent verrucae.
F. Ventral verrucae.
G. Numerous setae on prolegs.
H. Two verrucae on ninth abdominal segment.
I. Small tuft of tubercles on ventral posterior aspect of anal segment.
J. Pigment on spiracles.
K. Markedly dominant setae in dorsal verrucae.
L. Dorsal-lateral segmental pigmentation.

The larvae of the six species listed below have been available for examination, and the results may be summarised in the following table, in which the letters indicate the features in the above list, and the plus and minus signs refer to the presence or absence of those features.

	A	B	C	D	E	F	G	H	I	J	K	L	*Levuana*	Zygaenid Y
Levuana iridescens	+	–	–	+	–	–	–	+	+	–	–	+		7
Zygaenid Y	+	–	–	+	–	+	+	–	–	+	–	+	7	
Artona catoxantha	–	–	+	–	–	+	–	–	+	–	–	–	6	5
Artona trisignata	–	+	+	+	–	+	–	+	+	–	+	+	7	4
Artona albicilia	–	+	+	–	+	–	–	+	+	–	–	–	6	1
Zygaenid X (*Artona* sp.) . .	–	+	–	–	+	–	–	+	+	–	–	–	7	2

The figures in the last two columns are obtained by totalling the number of respects in which *Levuana* and Zygaenid Y agree with each of the other species in turn. (Zygaenid X is an undetermined species from the Solomon Islands.)

It is clear from the table that as far as the total number of similarities is concerned *Levuana* agrees with *Artona* spp. as closely as it does with Zygaenid Y, though not in the same respects. Zygaenid Y, on the other hand, does not agree with *Artona* nearly so closely as with *Levuana*.

Many of the characters considered are of specific value only, and are not of value as distinguishing features between two different groups of species. Others refer to differences in degree only. In order to compare *Levuana*-like species as a group with *Artona*-like species it is necessary to neglect those characters marked E, G, H, I, J, and K, which must be regarded as specific characters only. The remainder may be tabulated in the same way as before.

	A	B	C	D	F	L	*Levuana*	Zygaenid Y
Levuana iridescens	+	−	−	+	−	+		5
Zygaenid Y	+	−	−	+	+	+	5	
Artona catoxantha	−	−	+	−	+	−	1	2
Artona trisignata	−	+	+	+	+	+	2	3
Artona albicilia	−	+	+	−	−	−	1	0
Zygaenid X (*Artona* sp.)	−	+	−	−	−	−	2	1

It is now apparent, after eliminating those features which are likely to serve to distinguish between species only, that *Levuana* and Zygaenid Y are much more closely allied to one another than either is to *Artona*-like species.

The larva of *Levuana* is described on pp. 84–96. Its most striking distinguishing feature as compared with *Artona* spp. is the possession of a fleshy anterior rim to the prothorax. This occurs also in Zygaenid Y.

Conclusion.—*Levuana* and Zygaenid Y are very probably closely allied to one another and are representatives of a natural group of Zygaenids which is distinct from the *Artona* group. At the same time, the striking similarities in all the more general characters of the larvae, such as shape, size, general structure, and habits, indicate that both the *Levuana* group and the *Artona* group have arisen from the same branch of the Zygaenid genealogical tree and that their common ancestor is less remote and more specialised than that of ZYGAENIDAE in general.

6. CONCLUSION

The relationship between Zygaenids of the *Levuana* type and those of the *Artona* type is evidently not nearly so close as the striking similarity between their early stages suggests. Nevertheless, this similarity is so great that it cannot be attributed to chance, nor can it be attributed to convergence. The explanation must be that *Levuana* and *Artona* have retained in their early stages an ancestral form which is common to both of them. In their more general characters, such as shape, size and habits, even the adults have retained some of the peculiarities of their ancestor, and the specialisation on different lines which the adults have undergone has not yet extended in any very marked degree to the early stages. The tibial spurs show that *Levuana* is more specialised than *Artona*, and the wing-venation further shows that *Levuana* is specialised in an entirely different manner from *Artona*, and, in fact, from nearly all other Zygaenids. The tibial spurs are not necessarily of value as an indication of natural affinities. There is a tendency towards the reduction of them in the family as a whole, and the absence of the same number of them in several different species does not necessarily indicate a close affinity between these species. The great assortment of insects included in the CHALCOSIINAE cannot possibly be closely related to one another, and the absence in all of them of the fore-tibial spur is a feature which must have been brought about by convergence. The spur must be either present or absent, so that it is not surprising that a number of insects that differ greatly in their wing-venations and other features within the limits of the family should converge in this one respect. There is therefore no reason to suppose that *Levuana* bears a closer natural relationship to the CHALCOSIINAE than to the ZYGAENINAE in general or to *Artona* in particular. On the contrary, it is very probable that *Levuana* is more closely related phylogenetically to *Artona* than to many, and probably most, other genera. Certainly the special case of *Levuana* and *Artona* implies that the present division of the ZYGAENIDAE into CHALCOSIINAE and ZYGAENINAE is an unnatural one, but until our knowledge of the early stages of the family is much more complete, a more satisfactory division is impossible, and the present system will remain the most convenient.

ORIGIN AND NATURAL HABITAT

ORIGIN OF LEVUANA-LIKE FORMS

The genus *Artona* is Indo-Malayan and is not known to extend farther east than Celebes. The genus *Homophylotis*, in which Jordan places *albicilia*, is, however, well represented in New Guinea and Queensland and extends to the Solomons, and *Homophylotis* is very closely allied to *Artona*, its wing-venation being specialised in exactly the same peculiar way. Moreover, *Homophylotis* shows the same general appearance, size, and habits in all its species as *Artona* and *Levuana*. It is therefore probable that the common ancestors of these forms inhabited the East Indian and Melanesian region, when these were joined by land connections. Although few other species which have diverged from the ancestral forms in the same manner as *Levuana* are known, it is most likely that several such species are to be found in New Guinea and the Solomons, where very little is known of the more insignificant Lepidoptera. We can further surmise from the distribution of the species that the specialisation of the *Levuana*-like species occurred in, and was peculiar to, the Melanesian Region.

Artona catoxantha is at least as old as the Glacial epoch, because it occurs with the same series of parasites on Java, the Malay Peninsula and Borneo, which were united into one land mass at that time, and it is probably much older than this.

The butterflies and moths are known from the fossil record to have been evolved to much the same extent as at the present day in the Cretaceous period, and it is probable, therefore, that the immediate ancestors of the Zygaenid *Heteropan* that is native to Fiji reached these islands with the migration of snakes and lizards. The powers of flight of *Heteropan*, like those of *Levuana*, are very restricted, and it is unlikely, therefore, that it arrived after the land bridge was broken.

It is probable that the immediate ancestors of *Levuana* and its allies were widely distributed between Malaya and Fiji at the time of a land connection at about the time of the upper Cretaceous period or a little later, and that when the submergence occurred in the Eocene or Oligocene these insects were left on the high points of land that became islands.

On account of the isolation, it is thought that in the time intervening between the submergence and the present day this ancestral stock has undergone a certain amount of differentiation. The reason for this assumption is that such differentiation is known to have occurred in the case of the insects entombed in the Florissant beds of the Oligocene period. Scudder has described over 700 of these insects, and although they have a very modern aspect, the species are extinct. In the case of oligocene ants that have been beautifully preserved in a tree resin in which they became embedded and which has since hardened into the material known as Baltic amber, the evidence is even clearer. Dr. W. M. Wheeler, who has devoted a lifetime to the study of ants, was unable to distinguish three of these amber fossil ants from living species. Of the forty genera represented, thirteen are now extinct and twenty-seven still living. It is thought, therefore, that the ancestral stock of the *Levuana-Artona* series was widely diffused when Melanesia was part of a great continent uniting with Malaya, but as will be shown below, it seems probable that *Levuana* itself did not reach Fiji until modern times.

The Natural Habitat of Levuana iridescens

Levuana iridescens is not known to occur anywhere outside Fiji, yet there is reason to believe that it is not native in Fiji. At the beginning of 1925, when comparatively little was known about it, it was thought likely that it might be native in Indo-China or thereabouts, but subsequent investigations, notably in Malaya, Java and the Solomon Islands, have shown that this cannot be the case. As a result of work in those countries, it is almost certain that no Zygaenids more nearly akin to *Levuana* than *Artona* occur there. A search was then made in New Guinea. The larvae of three different Zygaenid species were discovered there, and all these larvae bore a close general resemblance to *Levuana* and *Artona*, but unfortunately they were rare and proved most difficult to rear in captivity, with the result that no adults were obtained. We think it probable, in view of more recent discoveries, that all these were *Artona* spp., and certainly none of them were *Levuana iridescens*, but they served to direct our attention to New Guinea and the neighbouring islands as a possible home for *Levuana*. In 1928 a search was made for *Levuana iridescens* in the Solomon Islands, and although *L. iridescens* itself was not found, a great advance was made by the discovery of the closely allied species, Zygaenid Y. This is the only known Zygaenid which shows a closer affinity in all stages to *Levuana* than to *Artona*. The New Guinea species, *Leptozygaena gracilis*, which is probably closely allied to *Levuana*, is not known in its early stages, and its true affinities cannot be determined with certainty unless pupae can be obtained.

It is certain that Zygaenid Y is native to the Solomons, chiefly on account of its comparative scarcity and of the abundance of parasites attacking it. It is also certain that *Leptozygaena* is native in New Guinea. The natural home of *Levuana iridescens* is, however, still unknown, unless it be Fiji.

In the search for *Levuana* the study of food-plants and feeding habits has played an important part. All the Zygaenids which bear a general resemblance to *Levuana* and *Artona* make the same characteristic feeding-scars on their food-plants as *Levuana*, and this fact led to their discovery. Five species of *Artona* have been found feeding on Zingiberaceae (three in Java, one in New Guinea, and one in the Solomons), and three species of *Artona* have been found on palms (*A. catoxantha*), on coconuts and other palms in Malaya, Java, Sumatra and Borneo ; Zygaenid B on *Licuala* in New Guinea ; Zygaenid C on a palm similar to *Areca* in New Guinea. Zygaenid Y feeds on bananas in the Solomons, and *Levuana* on coconuts and other palms in Fiji. Of these, the two coconut-feeding species (*A. catoxantha* and *L. iridescens*) occasionally eat banana, but are never a pest on it.

Zygaenids which feed on Zingiberaceae are all *Artona* (*Homophylotis*) spp. The evidence available also indicates that *Levuana* and its nearest allies, as well as several species of *Artona*, feed only on palms and bananas. Coconuts and bananas are both of economic importance, and it is quite certain that if any Zygaenid in New Guinea and the Solomons fed on either, in sufficient numbers to become a pest, it would have been discovered by now. Special attention was paid to coconuts in the Solomons and all round the coast of New Guinea, north and south. In New Guinea, an abundance of old feeding marks of the characteristic Zygaenid form were found on sago palms (*Metroxylon* sp. ?) in a swamp near Aitape on the north coast. None of the insects responsible for them could be found, and it was clear that the outbreak had died out two or three months previously, probably owing to the wet season, during which all the Zygaenids found were very rare, although their feeding marks showed that they too had been much more common previously. The feeding marks on sago were not those of *Argaula* spp., which feed in a rather similar manner. In the Solomons Zygaenid-like feeding marks and an empty Zygaenid cocoon were found on one small coconut palm, but no larvae were present.

Artona-like species found in New Guinea on *Licuala* and *Areca* (?) apparently do not normally feed on coconuts, but they could probably do so if necessity arose, just as *A. catoxantha* and *L. iridescens*, which normally feed on coconuts in those countries where they are pests, can also feed on other palms and even bananas. It is therefore not unlikely that *L. iridescens* itself feeds normally on one of the native palms in the Solomons or in neighbouring groups of islands, and that it attacked coconuts in Fiji because its normal food-plant was not present there. There are many palms in the New Guinea region which do not occur elsewhere.

The chief reason for supposing that *Levuana* is not native in Fiji is that it had no parasites attacking it prior to 1925, when parasites were imported from Malaya. It is a well-established fact that an insect in its native habitat is controlled by natural enemies. *Artona catoxantha* and *A. trisignata* in Malaya and Java are always controlled by parasites long before they have exhausted the available food-supply, though they often do considerable damage to their food-plants first. All the other species discovered, including Zygaenid Y, the closest known relative of *Levuana*, are so efficiently controlled as to be comparatively rare. Yet *Levuana* in Fiji had no natural check at all. It continued its ravages in each locality until it was faced with food shortage, and then it sought food in other localities. It threatened to wipe out all the coconuts in Fiji.

Levuana first attracted attention in Fiji in the latter part of the nineteenth century. If it were native in Fiji without parasites, or even if it had been imported into Fiji only fifty years before that time, it would surely have wiped out all the coconuts long since. On the other hand, if it was formerly present with parasites or other controlling factors, the latter must suddenly have been suppressed towards the end of the last century so that *Levuana* suddenly multiplied to an indefinite extent without anything to check it ; and it is difficult to believe that natural controlling factors could be suspended comparatively suddenly in this way.

There is one other aspect of the problem which is worth considering. *Levuana* is allied to *Artona* whose home is in the Far East. It is even more closely allied to Zygaenid Y which is native in the Solomons. The insect fauna of the Far East is extremely rich, and that of the Solomons is also rich as compared with Fiji. The competition in insect life generally is very much greater than in Fiji. We should therefore expect an insect which is native in Fiji either to be less specialised than its allies in these other countries ; or else, if it is more specialised, to be so as a result of degeneration only. *Levuana*, however, is more specialised than *Artona*, even as regards those characters which are common to both, and it is specialised to the same extent as Zygaenid Y. Moreover, it shows no degeneration at all, as compared with *Artona* spp. and Zygaenid Y.

All these considerations, therefore, indicate that *Levuana* is not native in Fiji. If it is not native, we have to face the question of how it reached Fiji. We have already shown that the comparative morphology of the adults and larvae of allied species, together with the occurrence in the Solomons of Zygaenid Y, point to the New Guinea region as the natural home of the *Levuana*-like forms. There is a long succession of islands extending south-east of New Guinea towards Fiji, including the Bismarcks, the Solomons and the New Hebrides, but this chain of islands ends with the New Hebrides, and there are about 500 miles of open sea between the New Hebrides and Fiji. It is not unlikely that the *Levuana*-like forms are represented in all the islands from New Guinea to the New Hebrides, but it is quite certain that *Levuana* could not cross 500 miles of open sea, of its own accord, against the prevailing winds. Experiments have indicated that it cannot fly more than ten miles, and probably not nearly so far. We are therefore forced to the conclusion that it was accidentally imported into Fiji by boat or by hurricane about the middle of last century.

Even this conclusion presents many difficulties. The rearing of *Levuana* larvae in captivity is more difficult than that of most Lepidoptera, and it is most unlikely that the larvae would have a supply of fresh leaves available on a boat running from the Solomons or the New Hebrides to Fiji unless they came on the leaves of a small ornamental palm. The adult life is so short as to preclude the possibility of the adults being transported to Fiji, particularly as they would have no food on a ship. The only other stage in which *Levuana* could be imported accidentally into Fiji is the pupal stage. The cocoons are invariably formed on the food-plant, and therefore some part of the original food-plant with full-grown larvae or pupae on it must have been taken on board the ship. Sago, *Nipa* and coconut palms are used extensively by the natives for making baskets and other things, and might easily have been taken on board in that form.

Sufficient has been said to show that there are many serious objections to the theory of the accidental importation of *Levuana*, and it is difficult to believe that circumstances could have combined in such a way as to make such an importation possible. Nevertheless, in view of the evidence which has been cited, we find it very much more difficult to believe that *Levuana* is a native of Fiji, and are of the opinion that it is yet to be found either in the Solomons or the New Hebrides.

Food Plants

In addition to the coconut palm, which is the preferred food of *L. iridescens* in Fiji, the native sago palm (*Sagus vitiensis*) is freely resorted to by the moth. Some investigators of the *Levuana* problem held that the sago palm was really its preferred food-plant, a fact obscured by the rarity of this plant as compared with the coconut. But it is interesting that at the present time, when there is no question of pressure by food shortage, *Levuana* is still feeding on coconuts, so that the latter plant is almost certainly its first choice of food.

During bad outbreaks, when there were swarms of moths on the wing after each brood and the supply of coconut food became limited locally, other plants would be attacked, but never to any great extent.

The immature stages have been bred right through on banana; but sugar cane, rice, maize and a common orchid have also been recorded as occasional food-plants, although the moth will not breed through on any of the four last-named plants.

A native palm, *Veitchia joannis*, known as the "Niu Sawa," is another food-plant on which the moth can breed successfully. It is interesting that on this plant the larvae will only feed in the basal quarter of each leaflet, owing to the fact that the more distal part is not concave ventrally and affords no protection to the larva from sun or rain (see Plate XXI, Fig. C).

There are several species of bush palms on which *Levuana* might feed were they grown in the open; but the moth is not a shade-loving insect, and it was very seldom found on coconut trees surrounded by a secondary growth of native forest.

In places where various palms were planted for ornamental purposes, *Levuana* frequently resorted to such plants after the rather limited supply of coconut food was exhausted.

In Suva the Royal Palms (*Oreodoxa regia*) were always attacked. In the Botanic Gardens an inspection was made of the several palms in May 1926, and undoubted feeding marks of *Levuana* larvae were found on the following plants in addition to those mentioned above: *Oreodoxa oleracea*, *Areca catechu* (Betel nut), *Livistona chinensis*, *L. speciosa*, *Sabal palmetto*, *Elaeis guineensis*, *Actinophloeus macarthuri*, *Guilielma speciosa*, and an undetermined soboliferous palm with scale-covered fruits in huge pendulous compact spadices.

Larvae were fed in captivity successfully on the leaves of *Pritchardia pacifica*, although no signs of attack on that palm were noticed in the Botanic Gardens.

NATURE OF THE DAMAGE DONE BY LEVUANA

It is during its larval stage that the *Levuana* moth is a pest on coconuts. The larvae feed on the leaves of the palm, eating away all but the epidermis and cuticle.

Feeding is usually confined to the underside of the leaves, but so far as the damage to the plant is concerned, an equally detrimental effect is produced when either the upper or under surface of the leaf is eaten away.

Complete devitalisation of a leaf will result when 45 per cent. of the surface has been destroyed by larvae, owing to the fact that the uneaten tissue between the feeding scars soon rots away when the latter are fairly closely approximated.

We describe elsewhere the characteristic shape of the feeding scars, and will only consider here the morphology of the feeding scars in relation to the plant and the various changes undergone in them during the period subsequent to their formation.

The coconut leaf consists of the following tissue layers in order from the upper to the lower surface :—

1. Upper epidermis and cuticle.
2. Pallisade parenchyma.
3. Spongy parenchyma.
4. Lower epidermis and cuticle.

The vascular strands with supporting fibres which form the veins of the leaf are interspersed amongst the parenchyma (Fig. 12).

Levuana feeds on the parenchyma of the leaf, but to get at this, it eats away either the upper or (more usually) the lower epidermis and cuticle. All except the larger leaf veins are eaten through by the larvae, these remaining veins forming a close network across the inside of the scar.

A newly hatched larva is only capable of biting part of the way through the parenchyma so that the scars of such larvae are not transparent.

After a larva has fed, its feeding scar becomes surrounded by a deposition of callus tissue, the cells becoming gradually filled with a brown substance until their cavities are completely blocked up. Cells of the vascular tissue become calloused as well as those of the parenchyma (Fig. 13).

This callus tissue forms a brown line round the edge of the scar and is first visible about a week after the scars are made.

Inside the callus band there is an accumulation of pulverised cell walls. These turn brown a day or two after the scar is made.

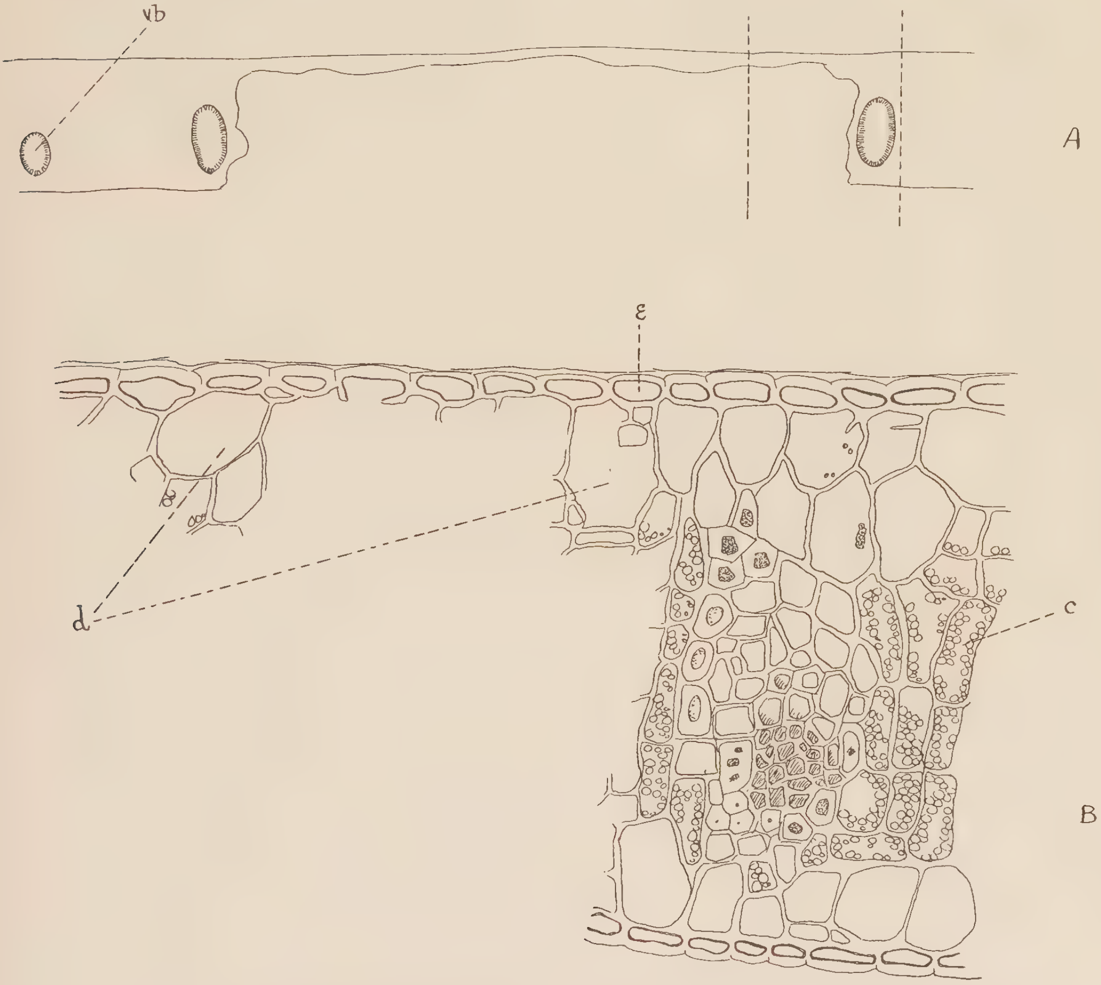


FIG. 12.—*Levuana iridescens.*—Freshly made feeding scar of fifth-stage larva through coconut leaf. A. Diagram of complete scar in transverse section ; *vb*, leaf vein. B. Enlargement of portion of scar limited by broken lines in A ; *c*, pallisade parenchyma containing chlorophyll ; *d*, cells which die and form brown dust which gets blown out by the wind in old scars ; *e*, upper epidermis.

Thus feeding scars assume a rich brown appearance after a few days, which gradually becomes less and less intense owing to the dislodgment of the pulverised lining of the scar by the action of the wind. After all the pulverised cell tissue has been blown out nothing remains in the scar but the colourless epidermis and cuticle of the opposite surface, which together form a parchment-like covering to the scar. In this condition, which in sheltered localities may not be reached till nearly twelve months after the scars were made, the scars appear on the tree as white streaks.

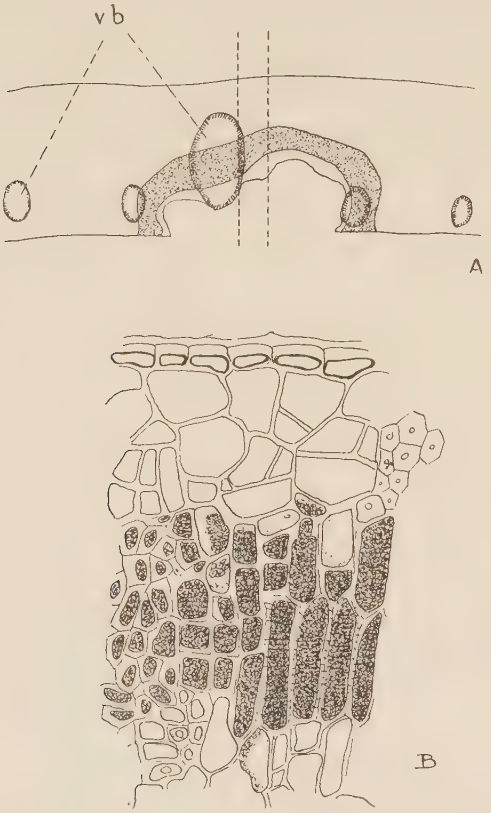


Fig. 13.—*Levuana iridescens.*—Feeding scar of newly hatched larva on under side of coconut leaf. A. Transverse section through feeding scar six months old, to show position of callous tissue (shaded) round edge of scar; *vb*, leaf veins. B. Enlarged view of portion of leaf between parallel lines in A. The callous tissue is developed both in the pallisade cells and in the small fibre cells of the leaf vein.

The final stage in the history of the scar is the rupture and removal of the white covering by the continued action of wind, leaving nothing but an open slit in the leaf.

Thus there is a gradual change in the appearance of trees attacked by *Levuana*, and although varying wind conditions make it impossible to lay down any fixed period for the "bleaching" of scars to become complete, yet by a close scrutiny of defoliated leaves in series one can ascertain the limits reached by a previous outbreak, and so decide whether recent feeding is the result of a flight from other trees or due to the survival and subsequent increase of the moth on the particular tree in question.

We found it possible with the aid of field glasses to determine with fair certainty whether larvae were still feeding on a high tree by the appearance of the leaves attacked. It is not easy to describe the exact appearance of such a leaf, but its colour is about halfway between the deep green of a healthy leaf and the rich copper colour of leaves which have only recently been defoliated; also the tips of the leaflets droop to a certain extent when the larval infestation is at all heavy.

The leaves of a tree in an outbreak area subject to average infestation by *Levuana* undergo the following colour changes :—

Before attack—green.
After attack—pale green
↓
greeny brown
↓
copper colour
↓
pale brown
↓
grey
↓
white.

PLATE III

APPEARANCE OF COCONUT PALMS AT THE HEIGHT OF AN OUTBREAK OF *LEVUANA*

This shows complete defoliation of the coastal band of coconuts in two neighbouring embayments on the island of Ovalau. At this stage there are scarcely any green leaves, the dead foliage being ash grey in colour. The degree of shock to the trees due to such defoliation is indicated by the fact that at the normal rate of a leaf per month it will take these trees thirty months to acquire a new set of green leaves.

PLATE III

The heaviest defoliation is produced in the areas where the trees are planted very close together, or, rather, in the usual native way, just left to grow up where they seed themselves. These conditions are typical of most of the coconut land on the islands of Ovalau, Moturiki, Naigani and Leleuvia.

During the four years prior to the introduction of *Ptychomyia*, when *Levuana* had spread over these islands, the trees in many localities were completely defoliated by the moth three times in succession; and although the vitality of a coconut tree is considerable, many trees which were growing in poor ground died as the result of the repeated attacks. This could be well seen in an area of rather swampy ground in the centre of Naigani towards the end of 1925, where all stages in the stunting of the foliage and final death of the trees was evident (Plate IV). On the other hand, on the rich flats of the Lower Rewa, occasional trees in bearing could still be found even after subjection to attacks of the moth for more than fifty years. In this locality, however, the trees are more scattered than on Ovalau and its neighbouring islands, and it is probable that defoliation of individual trees never became quite so complete as it did during the initial outbreaks on Lomaiviti.

After a tree has been completely defoliated, the new leaves, which are put out at a retarded rate, become very stunted, giving the tree a flat-topped appearance like a cabbage (Plate XX, Fig. A). When the leaves are undersized, the tree ceases to bear spathes, so that it takes about two years for a tree to recover its leaves and start to bear fruit after it has been completely defoliated.

The diameter of the trunk also diminishes when defoliation is severe: and with an outbreak of *Levuana* the decrease in the girth of the trunk is generally sufficiently rapid to leave a well-marked constriction in the trunk which becomes visible a few years after the conclusion of each outbreak and is a characteristic feature of "Levuana trees." Such a trunk constriction (see Plates XI and XII) could, of course, be caused by agencies other than *Levuana* which bring about the rapid defoliation of a tree, *e.g. Aspidiotus destructor*, *Promecotheca reichei* or fire; but when a number of a marked trunk constriction synchronises over a wide area it is an almost certain indication of a former *Levuana* outbreak.

It seems convenient here to draw distinction between the attacks of *Levuana* and of other coconut-leaf feeding insects in Fiji with which they might be mistaken. Only two such insects call for remark. These are *Promecotheca reichei*—the leaf-mining beetle—and the small brown moth, *Agonoxena argaula*.

The latter is the only coconut-leaf feeding insect whose scars somewhat closely resemble those of *Levuana*. We have more than once met planters who have been beguiled into believing that *Levuana* was on their plantations by this ubiquitous and relatively innocuous insect.

But typical scars of *Agonoxena* (cf. Plate XXIII, Figs. D and F) are of varying width and much less regular in outline than those of *Levuana*, although, like those of the latter insect, they follow the course of the leaf veins. Furthermore, *Agonoxena* spins a slender web over itself when feeding, and traces of this web are often noticeable even on fairly old scars. *Levuana* never spins any web.

From a distance, an outbreak of *Promecotheca reichei* might be mistaken for one of *Levuana* in so far as the leaves of the attacked trees in both cases assume a rich reddy-brown colour when newly defoliated. But any doubt as to which insect is responsible for the particular damage in question is at once dispelled by a careful inspection of the leaves—either with the aid of field glasses, or, better still, examination of a few damaged leaflets cut from an infected tree. The scars of the beetle are mines between the two surfaces of the leaf, whereas those of *Levuana* are always surface marks.

LIFE-HISTORY

1. Methods of Study.—Although *Levuana iridescens* will mate quite readily in captivity, it is only on rare occasions that it will lay fertile eggs under such conditions ; thus the chances of breeding a complete generation in captivity are remote unless a very large cage built round a growing coconut palm is used, when it often becomes rather difficult to keep a careful check on various individual larvae.* Therefore, our studies of the life history in the laboratory did not allow of the complete life cycle of any one individual being made.

Incubation period records were obtained from time to time in the field when moths were seen in the act of oviposition ; whereas the other immature stages were worked out by breeding larvae and pupae in captivity from eggs collected in the field.

To supplement these observations, some records were made of the duration of the variation stages with their successive broods of the moth inside a large wire-netting cage of fine mesh, built so as completely to enclose a small coconut palm about 14 feet high (Plate X, Fig. C).

In spite of the fact that by this means a fairly close approximation to natural conditions was made, a large number of the moths which emerged made their way to the sides of the cage and never laid eggs on the palm leaves. But, so far as the early stages were concerned, conditions of feeding and exposure to climate were the same as in nature.

The following methods were tried for breeding the larvae in the laboratory or insectary :—

1. In glass tubes plugged into cotton wool : fed with coconut palm leaf supplied fresh each day.
2. On freshly cut palm leaf kept in a test-tube of water under a bell jar : the mouth of the tube plugged with wool to prevent the larvae from falling or crawling into the water.

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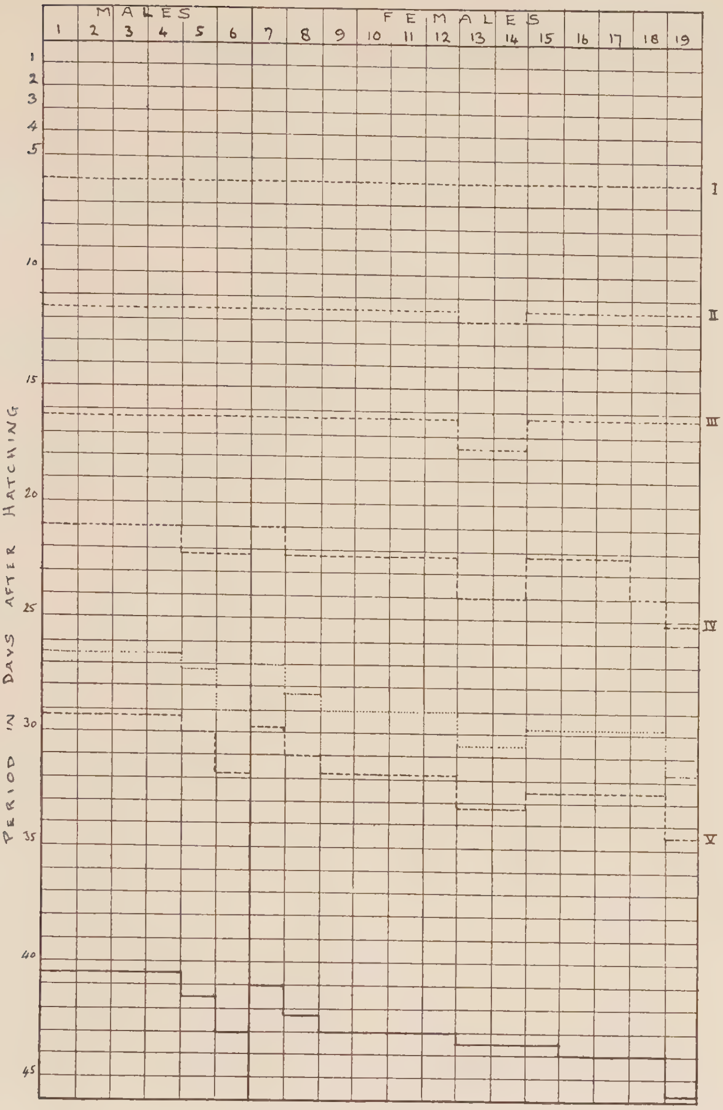
* Jepson bred it through in a cage in 1915, but there is no mention as to what were the dimensions of his cage.



	Max.	Min.	Mean
First instar	6	6	**6**
Second instar	6	5·5	**5·5**
Third instar	5·5	4·75	**4·75**
Fourth instar	9	4·75	**6**
Fifth instar	7·5	5	**6·5**
Prepupal period	2·75	2·75	**2·75**
Pupal period	11·75	10·25	**11·25**
Total larval period . . .	34·5	29·25	**31·5**
Period in cocoon	13·75	12·5	**13·5**
Hatching of egg to adult emergence	45·75	40·5	**42·75**

Summary of Stages [figures are days].

FIG. 14.—Diagram illustrating the relative duration of the larval stages and pupal period of nineteen *Levuana iridescens* (6 ♂♂, 13 ♀♀), all hatched from the same egg mass in July, 1926 (see text, p. 70).

3. On small seedling palms potted up in empty 4-gallon kerosene tins, kept inside the insectary.
4. On small palms as in 3, only kept in the open.

Methods 1 and 2 were unsuitable for breeding first and second stage larvae because the latter are at that time extremely sensitive to conditions of food and moisture, and even the few larvae which did not actually die when reared in this manner would show a great lengthening of the instars as compared with others kept as controls on growing palm leaf.

On the other hand, for more mature larvae, these methods were quite as successful as any other, and they had the decided advantage that there was no necessity to remove the larvae from their food when needed for microscopic examination.

Methods 3 and 4 were found most suitable for breeding young larvae; but even on the growing palms there was often a large mortality amongst first instar larvae some three or four days old if kept indoors—attributed to an inconstant moisture supply—whereas predators took their toll of the larvae when kept out of doors.

The method finally decided on for feeding the larvae in these experiments (this method has been employed, except where otherwise stated, for all the larvae whose development is recorded in Figs. 14, 15A and 15B) is in the nature of a compromise. It seemed to remove as far as possible the discrepancy which must always exist between field and captivity conditions.

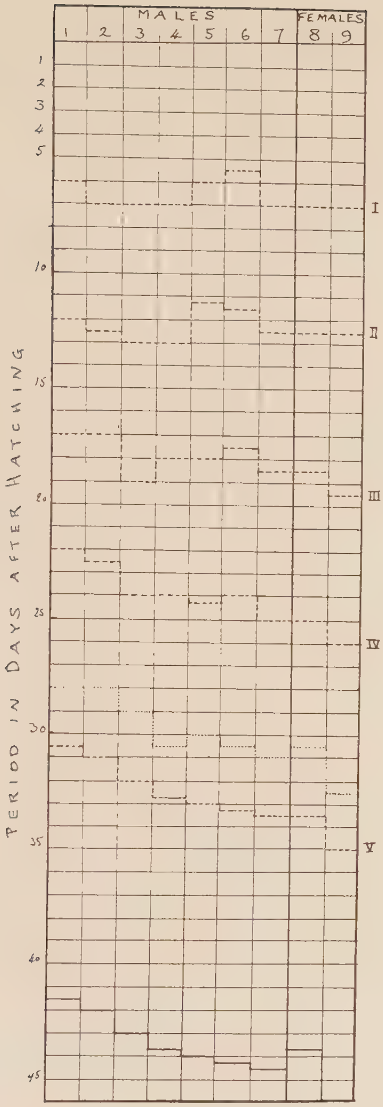
Eggs were collected from the field, and each mass was pinned on to a separate leaf of a small potted coconut palm. The latter would then be ringed with tree tanglefoot to prevent the access of ants, and then placed out of doors until the larvae were ready to undergo their first ecdysis. Palms were then moved into the insectary.

After the second moult the larvae were removed from the palm and each placed in a separate numbered tube with fresh-cut coconut leaf supplied daily. In this way it was possible to study the development of each individual larva without chance of confusion, since it is only after the second moult that the duration of the instars begins to show appreciable variation between different larvae from the same egg mass.

2. The Early Stages.—The seasonal variation in temperature, small though it is, plays an important part in determining the duration of the immature stages of the moth.

In Fig. 16 are given the temperature means, tabulated and plotted in a graph, for the months of 1925, 1926 and 1927, during which time all our work on the life history of *Levuana* was carried out.

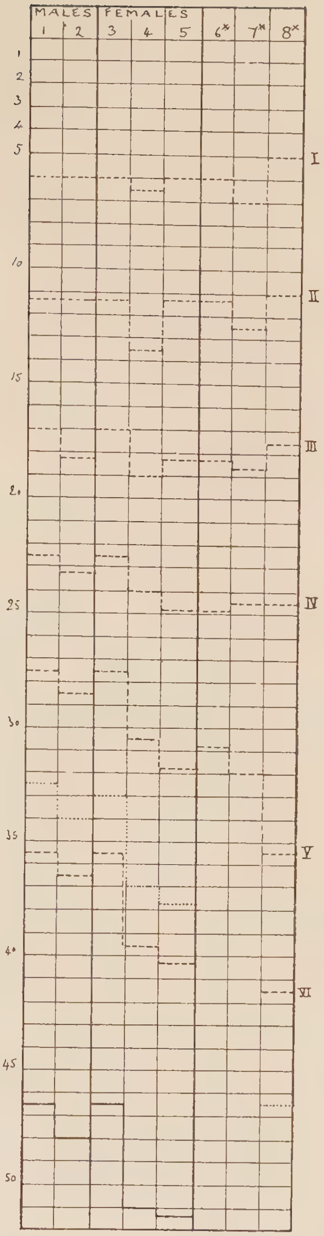
Our laboratory experiments to determine the duration of the early stages were all done in the cool season, so that no detailed comparison with the various early stages of a hot season brood can be made. But from records kept in the large wire cage mentioned above it appears that there is a difference of some eight to ten days in the duration of the early stages between " summer " and " winter " broods in an average year.



	Max.	Min.	Mean
First instar	7	5·5	**6·5**
Second instar	6	5·25	**5·5**
Third instar	7	4·5	**6**
Fourth instar	6·5	5	**6**
Fifth instar	6·5	5	**6**
Prepupal period	3	2·5	**2·75**
Pupal period	11	10	**11**
Total larval period . . .	35	30·5	**32·75**
Period in cocoon	13·5	12·75	**13**
Hatching of egg to adult emergence	46	41·5	**43·5**

Summary of Stages [figures are days].

Fig. 15a.—Diagram illustrating the relative duration of the larval stages and pupal period of nine *Levuana iridescens* (7 ♂♂, 2 ♀♀), hatched concurrently from various egg masses in July, 1926 (for explanation, see Fig. 14).

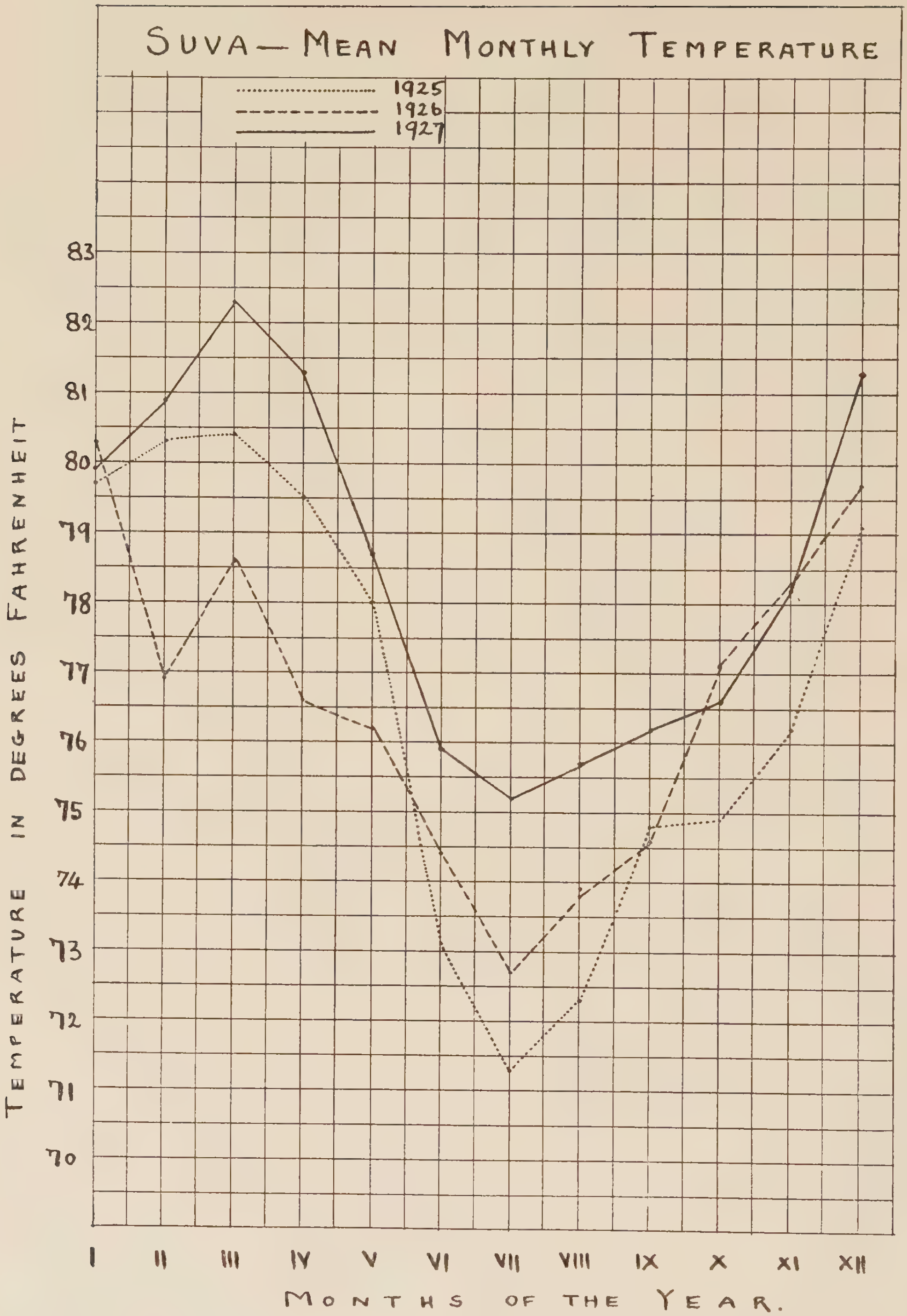


	Max.	Min.	Mean
First instar	7	5	**6**
Second instar	7	5·25	**5·5**
Third instar	7	5·5	**6·25**
Fourth instar	7	5	**6**
Fifth instar	11	5	**6·5**
Sixth instar	6·5	5	**5·75**
Seventh instar †	5	5	**5**
Prepupal period	3	2·5	**2·5**
Pupal period	11·5	11	**11**
Total larval period . . .	40·25	35·5	**37·5**
Period in cocoon	13·5	13	**13·25**
Hatching of egg to adult emergence	51·25	46·5	**48·5**

Summary of Stages [figures are days].

* Died before completing development.
† Only one instance.

Fig. 15b.—Diagram illustrating the relative duration and number of the larval stages and pupal period of *Levuana iridescens* (from various egg masses) which underwent an abnormal type of development (for explanation, see Fig. 14 and p. 71).



	1925	1926	1927	**Av. 30 years.**
January . .	79·7	80·3	79·9	**79·9**
February . .	80·3	76·9	80·9	**80·5**
March . . .	80·4	78·6	82·3	**80·1**
April . . .	79·5	76·6	81·3	**78·8**
May . . .	78·1	76·2	78·7	**76·5**
June . . .	73·1	74·4	75·9	**74·8**
July . . .	71·3	72·7	75·2	**73·6**
August . . .	72·3	73·8	75·7	**73·7**
September . .	74·8	74·6	76·2	**74·5**
October . .	74·9	77·1	76·6	**76·0**
November . .	76·2	78·3	78·3	**77·3**
December . .	79·1	79·7	81·3	**78·9**

FIG. 16.—Monthly mean temperatures (in ° F.) in Suva for the years 1925, 1926 and 1927 : also the average over a period of thirty years.

Then again it was found that the conditions under which breeding experiments were carried out governed the length of development to such an extent that it was necessary to do repeated experiments in order to be certain that, in cases of protracted development, conditions of food and moisture were not alone responsible.

Thus in selecting the following records of the early stages great care has been taken to eliminate those instances where it is considered that a pathological condition had been produced by breeding in captivity.

3. The Incubation Period.—The incubation period of the eggs of *L. iridescens* ranges from six to nine days, the higher figure being obtained during the cool weather of June and July 1925.

Jepson, in 1911, says: "Larvae make their appearance from the egg in about four or five days" (after oviposition), but he precedes this remark by the statement: "The life history is rather obscure, but so far as one can say at present is somewhat as follows."

In later experiments, 1915, the same observer says: "Incubation period invariably 7·5 days," but he does not contradict the earlier record in any subsequent report as far as we can find. Lea, in 1924, confirms Jepson's later record by incubation period readings of from seven to eight days. We have never come across an incubation period of less than six days and feel inclined to doubt Jepson's earliest record.

There is only very slight variation in the incubation period between eggs of the same mass. With few exceptions, all the fertile eggs of one mass hatch within an hour of each other. In the few cases where the hatching of an egg was markedly delayed, the larva invariably proved to be pathological, and often failed to emerge completely from the chorion.

The average period of incubation for fifty egg masses taken in various localities and at all seasons was 7·25 days—the eggs usually hatching on the eighth day after oviposition.

It was observed on several occasions that nearly all the eggs laid on a certain tree by one brood of moths would require the same period for incubation. This was tested experimentally by examining the hatchings of the eggs of successive broods inside the large wire cage during the latter part of 1926—*vide* following table.

TABLE SHOWING INCUBATION PERIOD FOR THE EGG MASSES OF THREE SUCCESSIVE BROODS OF *L. IRIDESCENS*, INSIDE LARGE WIRE CAGE—1926.

Brood.	Percentage of egg masses.	Incubation period.
October . . .	100	8 days
November . . .	100	6 ,,
December . . .	86 14	8 ,, 7 ,,

It will be noted that although the mean temperature for November was slightly lower than that for December (*vide* Fig. 16), yet the shortest incubation period, *viz.* six days, was recorded in the former month. Moreover, eggs kept inside the insectary, where the temperature was always one or two degrees in excess of that outside, did not hatch before those kept as controls in the open.

Thus, although the average incubation period seems to be longer in the winter than in the summer months, by subjecting egg masses to but slight differences of temperature no marked effect on the incubation period has been observed.

No experiments were done to test the limits of temperature within which eggs would hatch. Such experiments can have very little value when one is dealing with an insect which is hardly likely to be required for shipment to another country.

4. The Larval Stages.—Figs. 14 and 15A illustrate the variation in and length of the larval stages and pupal period of *L. iridescens* in the cool season.

In Fig. 14 all the larvae emerged from the same egg mass and were all bred during June and July 1926, whereas in Fig. 15A the larvae were derived from various egg masses and were bred during the months April to July 1926.

In the case of numbers 1, 2, 3 and 6 of Fig. 15A, the larvae were not transferred to tubes, but were kept on separate palms until they pupated. As, however, there was no appreciable difference in the duration of the instars between those kept throughout on palms and those transferred to tubes, it shows that the latter method of breeding did not induce a lengthening of the development and could therefore be relied on to furnish the required conditions.

All the larvae were examined twice a day, and by this means it was possible to ascertain the time of each moult to the nearest six hours, since there is always a brief resting period—about six hours—after each moult before the larva starts to feed. Thus, in the figures the horizontal lines indicating larval moults, etc., are drawn so as to illustrate the duration of the instars to the nearest quarter day.

A summary table of the range of and mean periods of the various stages is given in each figure for the larvae concerned.

We think it desirable to distinguish as a separate stage that part of the final instar, known as the prepupal period, during which the larva ceases to feed and spins its cocoon within which it lies dormant until the last larval skin is shed. Our figures for the fifth instar are in all cases exclusive of this period.

In previous records of the early stages of *Levuana* the pupal period has been reckoned as from the time the larva spins its cocoon * ; but it does not actually pupate until some forty-eight hours have elapsed after completing the cocoon. As it is quite possible to remove the newly formed cocoon without damaging the insect, one can ascertain the exact time at which pupation takes places. Our pupal periods are thus exclusive of that part of the last larval instar spent within the cocoon. Furthermore, the figures for the total larval period are inclusive of the prepupal period and are based on a number of single individual records.

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* With the possible exception of Jepson's record of seven days in 1911.

It will be noticed that in the early instars there is more variation amongst the larvae from different egg masses than amongst those from the same egg mass, but that taken as a whole the range in duration of the various stages is not a great one.

Besides checking the moults, it was possible to ascertain the amount of food each larva had eaten from day to day and, therefore, to select only those larvae which fed in a normal way for inclusion in our appended figures of the larval stages. For, whereas a larva normally feeds every day (excepting during those periods of inactivity immediately preceding and succeeding a moult) it was sometimes found that, in spite of having an ample food supply, a larva had not fed for a whole day, and in all such cases this was followed up by an abnormal lengthening of the instar, and in some cases death. In two cases, however, such larvae managed to survive their voluntary fast without any serious consequences, and, for the sake of interest, these are included in our records. No. 19 of Fig. 14 and No. 9 of Fig. 15A did not feed at all on the twentieth and seventeenth days respectively after hatching. Other larvae fed every day in a normal manner, and all were given equal chances to feed.

Even this one-day fast had, as can be seen from the figures, a lengthening effect on the instars of these two larvae, and their total development was in each case more than a day longer than that of any of the rest. Thus it will be seen that lack of food for even a day may have a far-reaching effect on the duration of the subsequent instars and, as the brood period of *Levuana* in the field is controlled by the rate of development of the mass of individuals which usually have access to an abundant food supply, it is necessary here to confine our attention to such individuals as display normal habits in order to obtain the exact counterpart of natural conditions.

The average length of the early stages is longer in the female than the male, as seems to be usual with most Lepidoptera, this increase being accounted for by a lengthening of the last larval instars rather than of the pupal period.

A large number of incomplete life history records have been made from time to time in the course of studying the morphology of the early stages. These are not presented here in full because it is thought that the data obtained by the more complete rearings set forth in Figs. 14 and 15A represent an average life history of *Levuana* in the cool season. But there are amongst these other records instances of both longer and shorter instars than those of our figures, so we think it advisable to place on record here the following data giving the maximum and minimum for each respective stage.

Table showing Variations in Life History for Various Months of the Years 1925 and 1926.

	Maximum.	Minimum.
First instar . . .	7 days *	4 days (xii/26; v/25)
Second instar . .	7·5 ,, *	4 ,, (xii/26; v/25)
Third instar . . .	7·5 ,, *	4·5 ,, (v/25)
Fourth instar . .	7 ,, (v/25)	3·75 ,, (v/25)
Fifth instar . . .	15 ,, *	4 ,, (v/26)
Prepupal period . .	3 ,, (v/26)	2 ,, (v/26)
Total larval period .	42 ,, *	25·5 ,, (xi/26)

* Larva was bred from the egg in a jar with cut leaf as food, iv/25.

All the larvae whose instars are quoted in the above table were observed to feed every day, so that although these records depart from the average by a wide margin, yet they represent what are probably perfectly normal, if rare, occurrences in the field. The larva, which was reared in a glass jar in April 1925, and which had such a long larval life, matured to a perfectly normal male moth, but as this took place during one of the hotter months, we must attribute its much-lengthened development entirely to the unsuitable nature of its food.

Amongst the figures given in the above table there are some hot season records. The total larval period of 25·5 days in November 1926 affords a striking contrast to the thirty-two day records of the previous July.

In the early records of the life history of the moth there is no mention made anywhere of the various larval stages having been studied, all the figures being for the total larval period.

Unfortunately, except in one instance, there is no mention made of the months during which the observations were made; but the figures mostly lie within the range of those quoted above for the hot and cool seasons of 1926.

We have been able to find the following records :—

1. Jepson, 1911, larval period twenty-one * to twenty-eight days.
2. Jepson, 1915, larval period twenty-seven to thirty days.
3. Simmonds,† IV, 1923, larval period twenty-eight days.
4. Lea, 1924, larval period twenty-seven to thirty days.

5. The Pupal Period.—As in the other immature stages there seems to be a seasonal variation in the length of the pupal period of *L. iridescens* due to changes of temperature; but the pupal period of the individuals of one brood is remarkably constant, *vide* Figs. 14 and 15A, where the range is but from 10 to 11·75 days.

The maximum and minimum for this stage, based on records which we have kept at all seasons, were twelve and seven days respectively.

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* We think that this is a doubtful record.

† Communicated to us by Mr. Simmonds from some unpublished notes.

In hot weather the adults generally emerge on the morning of the ninth day after pupation (*i.e.* the last larval moult); whereas in the cooler months emergence usually occurs on the eleventh or twelfth morning after pupation: the total period within the cocoon being from 12·5 to 13·75 days. This confirms the previous records of Jepson (1915), Simmonds (1923) and Lea (1924), where their figures (ten to fourteen days) refer to the total period within the cocoon.*

It is rather remarkable that out of fifty observations of the pupal period of *L. iridescens* females should average one day less than males. It seems probable that this is merely a coincidence, since there is as much variety in the duration of the pupal stage in either sex, and in nature there is a decided predominance of males amongst the first lot of moths to emerge in each brood.

6. Summary of Early Stages.—There is a variation, amounting to some eight to ten days, in the duration of the immature life of *L. iridescens* due to seasonal change of temperature.

A much more pronounced variation can be induced by unnatural conditions of breeding.

The mean periods for the various early stages of the moth in the cool season, compared with some inclusive figures for the same in the hot season, are given in the table below.

Jepson (1915) records the immature period as 47·5 to 51 days.

Simmonds (1923) records 44 days in April.

Lea (1924) records 47·5 to 55 days.

TABLE SHOWING MEAN DURATION OF THE IMMATURE STAGES OF *L. IRIDESCENS* IN THE HOT AND COOL SEASONS.

	Hot season.	Cool season.
Incubation	7·5 days	8·5 days
First larval instar		6·25 ,,
Second larval instar		5·5 ,,
Third larval instar		5·375 ,,
Fourth larval instar		6 ,,
Fifth larval instar		6·25 ,,
Prepupal period	2·75 ,,	2·75 ,,
Pupal period	8 ,,	11·125 ,,
Total larval period	25·5 ,,	32·125 ,,
Oviposition to adult emergence	43 ,,	51·5 ,,

7. Occurrence of Extra Larval Instars.—Although five is the usual number of larval instars in *L. iridescens*, this number is occasionally exceeded.

We can find no previous record of any such phenomenon in the local literature on *Levuana*; and in other ZYGAENIDAE, whose larval stages have been studied, the number is apparently always five. So that it was regarded with much interest that, during the breeding experiments conducted in Suva from May to July 1926, no less than ten out of forty-five larvae whose development was studied had more than five instars.

It was thought at first that such cases might be of perfectly normal occurrence; and since, owing to the intercalation of an extra stage, the characters whereby the usual five instars had been distinguished no longer held good, it was decided to make full investigation of the matter by noting the number of moults of larvae which hatched out on the caged palm, where conditions, for the early stages at any rate, were identical with those found in the field.

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* Jepson also records a seven-day pupal period in 1911.

But, although some dozen batches of larvae were carefully observed, no further cases of abnormal development occurred; so that we must now regard these extra larval moults as an abnormality, the cause of which is not fully understood.

In view of the fact that no cases of these extra larval moults have ever been observed in the field (although only comparatively few batches have been studied with this end in view), it seems possible that the phenomenon is in some way associated with the unnatural conditions of laboratory breeding, so that in describing the life history of *Levuana*, we have only considered typical five-instar individuals.

Three possible explanations of this phenomenon suggested themselves:

1. The number of larval instars determined by sex.
2. The forms which display this feature are "sports"—the progeny of one specific female, which itself displayed that peculiarity. In other words, there is a definite strain of *Levuana*, which has more than five instars; and that in a brood of the moth one would expect to be able to trace to the same egg mass any individuals that display this feature.
3. A pathological condition caused by unsuitable food, or any other physical factor.

Eight of the abnormal larvae were bred in the usual way from eggs collected in the field—their stages are recorded in Fig. 15B—and two were collected from the field as larvae and then reared in tubes to maturity. One of these last-mentioned larvae displayed all the characters of a typical second instar larva when it was collected; but in the laboratory it had five * more moults before pupation. The other larva was typically fourth stage when collected, but moulted three * times in the laboratory before pupation. One of these larvae gave a male moth, the other a female.

Moreover, two males and three females were bred from some of the larvae reared from eggs, so that any question of the extra instar phenomenon being connected with sex can be discounted.

Unfortunately, it was not possible to tell whether all the atypical forms had hatched from the same egg mass, because it was not until after pupation had occurred that their significance was realised. The palms on which they were bred had been stocked with more than one egg mass, all of which hatched concurrently, and as the object of the experiment was to determine the duration of the various instars it was not considered necessary to distinguish larvae from different egg masses, provided that they all hatched at the same time.

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* These numbers include the final moult when the larva pupated.

Thus we cannot be sure whether or not these atypical forms represent a distinct and constant variety.

Interest, therefore, lay rather in this direction of ascertaining the part played by some purely physical factor in the determination of this abnormal character ; but here, again, the evidence is somewhat conflicting.

Five larvae (Nos. 1, 2, 3, 5 and 6 *), whose development is illustrated in Fig. 15B, were all reared at the same time and in precisely the same way as a larva (No. 5) of Fig. 15A, which had the normal five-instar development.

Similarly larva No. 5 of Fig. 15B was fed in exactly the same way and at the same time as larvae Nos. 4 and 5 of Fig. 15A. Therefore, on this evidence, there is no reason to believe that conditions of breeding were responsible for the fact that six larvae should have had more larval instars than three others of the same batch. Furthermore, the two larvae collected from the field, mentioned above, had undergone their first few stages at least in natural surroundings, and when bred in the laboratory did not have any non-feeding days.

On the other hand, the remaining two larvae (Nos. 7 and 8 in Fig. 15B), which displayed this unusual feature, give support to the idea that possibly physical conditions are responsible.

Larva 7 of Fig. 15B was of the same batch (but not necessarily from the same egg mass) as larvae 2, 7, 8 and 9 of Fig. 15A. All these larvae were the sole survivors from fifty which hatched out from three egg masses pinned on a palm. Forty-five of the larvae died before completing their first instar owing to food conditions which did not suit them—probably due to an insufficiently constant supply of surface moisture on the leaf. But, as four out of the remaining five larvae underwent a typical development, what was it that caused unusual behaviour in the fifth larva ? The latter closely resembled the others until its fourth moult, after which it was smaller than the rest and also differed from them in other details of structure.

After this it continued to feed but very little each day and moulted again with very little accompanying change in form. During one day it bit at the leaf provided as food in no less than nine different places, but failed each time to eat away a strip more than 5 mm. long ; notwithstanding the fact that other larvae fed copiously on part of the same leaf in other tubes. It finally ceased feeding altogether and assumed the characteristic motionless attitude antecedent to a moult—its sixth since hatching. In this position it died very much shrivelled up. On dissection a fully formed head capsule was found within the skin, representing a seventh stage, which the larva never actually reached.

It is, however, worthy of mention that a larva from the same batch (No. 9, of Fig. 15A) also did not feed on one occasion ; but this had no other effect than a slight retardation of its development.

Another similar instance is the case of larva No. 8 of Fig. 15B. Here development up to the second moult was typical. After that it refused to

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* Crawled into the tanglefoot band on the palm stalk and died before pupation.

feed. This happened on four separate occasions during the remainder of its development; but between these spasms of voluntary starvation it fed quite normally. This larva moulted no less than six times, and was starting to make its cocoon when it was accidentally damaged while in the prepupal condition. But for this unfortunate accident, it would almost certainly have reached maturity, because there was nothing in its condition just prior to death to suggest that it was not perfectly healthy.

Summary.—Under laboratory conditions *Levuana* was observed to undergo on occasions an abnormal development with more than five larval stages. Ten out of forty-five larvae bred in May, June and July 1926 displayed this feature, and of these eight had six instars and two had seven instars.

The full explanation of this phenomenon was not discovered. It is possible that it may be aggravated—if not actually induced—by partial starvation.

It is found in both sexes, and there is insufficient evidence to assume that the individuals which display it belong to a distinct variety that breeds true.

By the intercalation of one or more extra larval instars, the period of larval development is prolonged to some five or six days more than the normal average.

With the exception that the characters used to distinguish the five instars are indecisive when applied to an atypical form, there is no morphological difference between the two types either in the larva, pupa or imago.

8. Adult Life.—The adult life of *Levuana iridescens* is a short one; no single case has been observed by us of a moth living for more than eight days.*

We conducted several experiments to ascertain the length of life of moths kept in captivity under various conditions; but although the moths would feed and mate, it was not possible to keep them alive for more than six days in the case of the male and five days in the case of the female.

Even in our large wire-netting cage adults never lived for more than four days. Food was offered them, firstly in the form of bunches of the blossom of " mile-a-minute " (*Mikania scandens*) on which adults had been observed feeding in the field; and when it was found that this did not attract them in the cage, honey and water solution was smeared over the fibre on which moths rest after emergence; but neither did this food attract them.

After emergence, the majority of the moths would fly up and settle on the top of the cage as if striving to get to the most illuminated part. In this position they were often killed by spiders, and in all probability lizards also took their toll. After a couple of days, if they had survived the attacks of predators, their wings would be so battered by their efforts to fly through the wire that they could scarcely rise from the ground and many would be carried off by ants.

When kept in a more confined space—for instance, a glass tube or jar—the vast majority died within forty-eight hours of emergence from the cocoon;

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* Lea gives a record of adult life as eleven days. He has since confirmed this in a letter and says he kept his specimens in large glass jars without food. He is not able to remember the sex of the moth which lived eleven days.

but occasionally they lived for longer, although this did not seem to depend entirely on whether feeding and mating had occurred—or oviposition in the case of the female.

TABLE SHOWING LONGEVITY OF *LEVUANA IRIDESCENS* ADULTS KEPT UNDER VARIOUS CONDITIONS IN CAPTIVITY.

	Date.	Mated.	Food.	Contained in—	Length of life.
MALES.	xi/26	?	None	Inside caged palm	4 days
	xi/26	?	,,	,, ,, ,,	4 ,,
	ix/26	?	,,	,, ,, ,,	2 ,,
	ix/26	?	,,	,, ,, ,,	2 ,,
	vii/26	No	Lantana blossom	Large glass jar	6 ,,
	viii/26	No	Diluted honey	,, ,, ,,	4 ,,
	vi/26	Yes	None	Glass tube	4 ,,
	xii/25	No	,,	,, ,,	1 ,,
FEMALES.	xi/26	?	None	Inside caged palm	4 days.
	xi/26	?	,,	,, ,, ,,	4 ,,
	ix/26	?	,,	,, ,, ,,	2 ,,
	ix/26	?	,,	,, ,, ,,	2 ,,
	ix/26	?	,,	,, ,, ,,	2 ,,
	ix/26	?	,,	,, ,, ,,	2 ,,
	viii/26	?	Diluted honey	Glass jar	4 ,,
	viii/26	?	,, ,,	,, ,,	4 ,,
	v/26	? Yes	,, ,,	,, ,,	2 ,,
	v/26	Yes	,, ,,	,, tube	2·5 ,,
	xii/25	No	None	,, ,,	3·5 ,,
	xii/25	,,	,,	,, ,,	2 ,,
	xii/25	,,	,,	,, ,,	2 ,,
	xii/25	,,	,,	,, ,,	1·5 ,,
	vi/26	,,	,,	,, ,,	1 ,,
	iv/28	,,	Honey solution	,, jar	5 ,,
	iv/28	,,	,, ,,	,, ,,	5 ,,
	iv/28	,,	,, ,,	,, ,,	5 ,,

The above table shows a few of the results obtained by experiments: very many more cases than those shown in this table have been observed when the total life has not exceeded two days.

These experiments to determine the adult life would appear to give a very poor conception of the truth under natural conditions.

In the large cage the moths, although exposed to usual field conditions of weather, are much more subject to the attacks of predators when they are resting on the wire netting sides of the cage (birds do not eat them much in any case), and their apparent diurnal phototropism overcomes their desire for food, which, under natural conditions, they probably all take. If, on the other hand, they are kept in a glass jar, the unnatural confinement might in itself seem to be sufficient to cause an abnormally rapid death. But the rather small number of observations of sufficient accuracy which we have been able to make in the field all point very decidedly to the fact that even under natural conditions the adult life of the moth is a short one; and does not, in the majority of cases, exceed by more than a day or two that obtained when moths are kept in captivity.

Up till the end of 1925, when *Levuana* was present in large numbers and in all stages at once, it was not easy to obtain the necessary conditions for making observations on the adult life. Moths were emerging continuously;

or if all the pupae were destroyed on a certain tree to prevent emergence for ten days, there was always the risk that larvae on the leaves would attract moths from the neighbouring trees ; and if the larvae also were removed, the moths whose life it was desired to study would probably forsake the tree from which they emerged and fly to other trees where larvae were feeding.

But after *Ptychomyia* had produced, by a phenomenally high parasitism, that restricted condition of the *Levuana* brood found everywhere after the middle of 1926, it was possible to obtain conditions suitable for experiments in the field.

At Nausori on 13th May, 1926, *Levuana* was plentiful both as adults, pupae and large larvae ; but the parasitism in the pupal masses was so high (more than 95 per cent.) that during the next ten days not more than an occasional moth could have emerged. On the above-mentioned date there were swarms of moths all over the trees ; many of these were quite newly emerged, judging by their completely undamaged condition, and yet six days later, on the 19th, there was not an adult moth to be seen anywhere. So that the moths observed on the 13th must either have all died or else have made off to another locality. It is very unlikely that the latter event occurred, because there was no shortage of food on the trees and the leaves were still stocked with larvae—now all fifth stage—which seem to attract the moths about to oviposit. Moreover, *Levuana* had been breeding for several generations on these trees, and there was no reason to account for their sudden departure.

Thus it seems reasonable to suppose that they all died in the interval without migrating ; and although some may have lived for longer than a week, we know that many did not live for more than six days.

One or two cases similar to that just quoted have been observed on Makuluva ; and the caretaker there, who notices the condition of the trees from day to day and is quite familiar with the moth, has frequently said that moths on the wing are to be seen for only a few consecutive days at a time ; since they do not migrate *en masse* from this small island they cannot live for more than a few days.

In addition to what has been said already, based on experimental work and field observations, there are certain facts about *Levuana* which all go to suggest that the adult life is very short. These are :

1. Oviposition begins within two days of emergence from the cocoon.
2. The eggs are laid in clusters ; therefore, oviposition is a more or less rapid process.
3. It is seldom, if ever, that one moth lays more than those eggs which are ready for laying on the second day after emergence.
4. Adults have very sluggish habits and generally partake in only short local flights, so that they fall ready victims to spiders and insect predators, especially to those that feed by night when the moths rest exposed on the fibre and leaves.
5. Very few badly battered moths are ever met with in the field ; it is thought that they must die before they reach this condition.
6. The moths do not undergo any seasonal hibernation in any stage.

In the extremely few absolutely reliable records of migatory flights, the moths probably took to the wing as soon as they were ready to oviposit, having discovered that in the locality where they passed their early stages there was no longer available green foliage on which to oviposit.

EGGS

1. Morphological Features.—The eggs of *Levuana* vary considerably in shape and to a less extent in size. The individual eggs of each cluster are usually all of approximately equal size although they may vary much in shape.

The measurements (*i.e.* maximum length and maximum width) of some hundreds of eggs from various egg-masses are summarised as follows :

	Max.	Min.	Mean.	
Length . .	0·86	0·69	0·75	millimetres.
Width. . .	0·53	0·46	0·50	,,

The most typically shaped eggs are perhaps those which are barrel-shaped, only with one end—the posterior — convex instead of flat. There is, however, so much variation in shape that it is of little use trying to generalise in this respect.

Fig. 17 shows the variation in shape of eggs drawn in the position in which they were laid on the leaf. We do not know to what extent the eggs of other Zygaenids display a similar type of variation. The eggs are normally laid with the longitudinal axis parallel to that of the leaf surface,* and although any surface of the egg may be attached to the leaf, attachment is usually by that surface which will be opposed to a lateral aspect of the enclosed embryo. There is a tendency for the uppermost surface to be depressed in the centre, although when that surface happens to be dorsal, the depression is often counteracted by the somewhat convex dorsal slide of the embryo. Even before the eggs leave the body of the parent, many of them have an arcuate form, owing to the curved nature of the basal part of

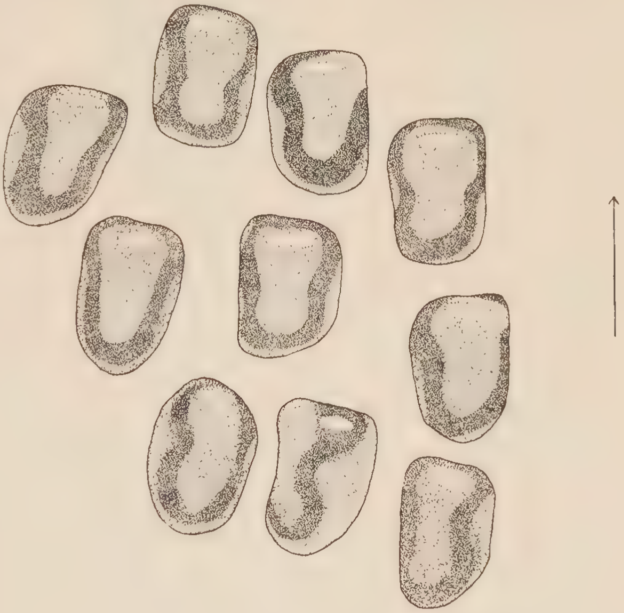

FIG. 17.—*Levuana iridescens* eggs, × 40.—Ten adjacent eggs of a four-day old cluster—drawn as they were laid on the leaf. To show the variation in shape and disposition of the pigment. The arrow indicates the micropylar (anterior) end.

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* Cf. Zygaenid Y, etc.

the ovarioles (see Fig. 71), and the concavity then present seems to persist after oviposition. When this concave surface lies uppermost, there is but a single depression ; but when it occupies some different position relative to the leaf, there are often two separate depressions noticeable.

Knowles * remarks on a depression ; but Lea adds the following note : " . . . depression present only shortly before the larvae hatch."

We think it probable that the last-named observer must have been referring to the concavity caused by the crinkling of the chorion, which invariably takes place twenty-four hours before hatching, since the depressions we refer to above can be clearly distinguished in newly deposited eggs, although that on the upper surface certainly becomes more pronounced as development proceeds.

The chorion is colourless, transparent and finely reticulate ; and although somewhat elastic, it is soft and easily crushed. The reticulation (see Fig. 18) is finer at the micropyle than over most of the remaining surface. It is, however, not possible to distinguish the micropyle by this feature alone, as there is a similar area of fine reticulation at the posterior pole of the egg.

Thus it is rather difficult to orientate the eggs when freshly laid ; in fact, until a fairly advanced stage of development is reached complete orientation is not possible, since the depressions referred to above are not sufficiently constant in position.

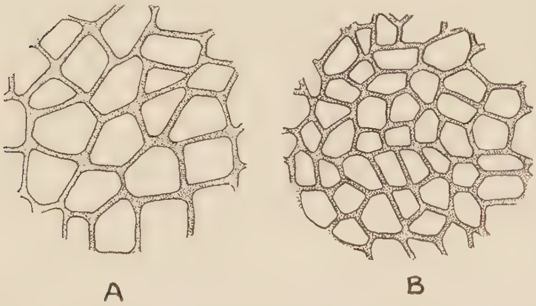

FIG. 18.—Reticulation of chorion of egg of *L. iridescens*, ×330. A. Over general surface ; B. At micropyle.

But partial orientation of an egg mass may be effected in the following way : In certain eggs of a cluster it will be noticed that one end is more convex than the other (see Fig. 17) ; this is the posterior end, and the micropyle will be situated in the centre of the opposite end. If this be determined for one egg, it will be sufficient for orientation of the whole cluster, since the remaining eggs will all point in the same direction.

It is not possible to see the micropyle with a lens because there is no specially conspicuous structure of the chorion around it, as is frequently found in other Lepidoptera ; but if eggs be treated in 10 per cent. solution of KOH and removed from the caustic before all the chorion is dissolved, it is possible to determine the exact position of the micropyle by strands of attachment from the chorion to the yolk globules.

2. Development.†—Eggs when newly laid are opalescent and almost pure white ; there is a faint marginal green tinge owing to reflected colour from the leaf. After twenty-four hours the margin of the egg becomes slightly more transparent owing to shrinking of the yolk.

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* " The eggs are small oval-shaped bodies with a depression in the upper surface."

† The development of the egg in the ovary is discussed on p. 130.

After a further period of some twenty hours pigmentation begins, and a band of pale red pigment can be distinguished showing through the transparent chorion. The shape of the band displayed uppermost varies in accordance with the position of the egg on the leaf (see Fig. 17). During the next two or three days * the pigmentation becomes more and more pronounced although still localised in a definite band ; two days before hatching, eggs appear almost entirely red to the naked eye, and are much less conspicuous on a leaf than when newly deposited.

The next stage is a gradual breaking up of the pigment band into separate spots. The latter form the dorso-lateral pigmentation on three body segments of the mature embryo. At the same time the chorion begins to assume a crinkled appearance and the egg loses its gloss which has been a characteristic feature up till now. The embryo now occupies the entire space inside the chorion and is curved in the manner shown in Fig. 19, B.

At this stage it becomes possible to distinguish the dorsal and ventral aspects of the egg, because the gland of the second abdominal segment is conspicuous as a dark spot in the posterior half of any egg which has lateral attachment to the leaf. Dorsal to this structure, is a short band of pigment (Fig. 19, A, *d.p.*) which is the line of tergal pigmentations of the larva.

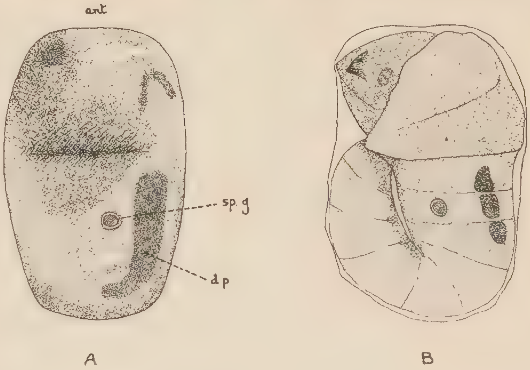

Fig. 19.—Eggs of *Levuana iridescens*, × 100. A. One day prior to hatching ; *d.p.* dorsal pigment band ; *sp.g.*, spiracular gland of second abdominal segment. B. Diagram of the fully developed embryo just before hatching : the egg treated with KOH until most of the chorion was dissolved away.

Hatching takes place somewhat less than a day from the time the pigment band commences to disintegrate.

The development of the egg may be briefly summarised thus † :

At oviposition . . .	glossy and uniformly white.
2 days after oviposition .	pigmentation begins.
5 ,, ,, ,, .	pigmentation reaches its maximum intensity. Egg still glossy.
6½ ,, ,, ,, .	pigment band breaks up into irregular patches, chorion crinkles and loses gloss.
7½ ,, ,, ,, .	hatching occurs.

3. Occurrence.—The eggs are laid in clusters on the leaves of the food-plant usually on the under surface of the leaf. But when food is scarce, it is no uncommon thing to find eggs laid on the upper surface of leaves. In extreme cases of food shortage we have found eggs on the outside of the unopened central leaf of a palm; but we have never found them on any other part of the food-plant, or on leaves which have been so completely defoliated that they no longer contain any living tissue.

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* Longer in the cool season.

† The periods given vary to some extent with the temperature.

Jepson remarks: " . . . the usual place selected for oviposition is at the base of the leaflets, although eggs may be scattered at random over the lower surface." We have found that there is no special place on the leaflets selected for oviposition, except in so far as moths refuse to oviposit on dead leaf tissue, and after a heavy defoliation by previous broods the basal angle of a leaflet is often the only part not eaten away.

The number of eggs in each cluster varies considerably. All numbers have been met with from eggs laid singly up to masses of between fifty and sixty. But, whereas *Artona catoxantha* lays its eggs singly or in groups of two and three scattered over the leaves, *Levuana* lays typically in compact clusters containing on an average about thirty eggs.

We have one record of finding a cluster containing eighty-four eggs; but close inspection showed that thirty-four of these eggs, all at one end of the mass, were of a greater average length than the remainder; and although all the eggs were at the same stage of development and similarly orientated, yet it seems probable that the mass was laid by two moths ovipositing simultaneously.

We think that *Levuana* usually lays all its eggs in one mass; but that a moth whilst in the act of oviposition often becomes disturbed or attacked by a predator,* with the result that its eggs are distributed in more than one cluster. This would partly explain the occurrence of clusters containing less than twenty fertile eggs, which number falls short of what we consider to be the average egg capacity of a moth—based on dissections of the ovary. Furthermore, data obtained from our breeding inside the large wire cage, supported by several observations in the field, show that undersized clusters may be also accounted for by the fact that sterile eggs are always laid in small clusters, *vide* the following table:

TABLE SHOWING THE NUMBER OF EGGS PER CLUSTER.

	No. of masses examined.	No. of eggs per mass.		
		Max.	Min.	Mean.
Field collections * . .	229	47	2	28
Inside cage—fertile . .	29	51	9	34
Inside cage—sterile . .	40	24	1	8

* These include counts made in various localities during 1925, 1926 and 1927.

It will be noticed that inside the cage, where there were comparatively few of those predators which normally attack the adult moths in the field, and where the wind was not strong enough to disturb moths while ovipositing,† the average number of fertile eggs per mass was thirty-four. This figure is remarkably close to that obtained from dissections of the ovary for the average number of fully formed eggs in a moth just prior to oviposition. Contrast this with the forty sterile masses where the average was only eight per mass.

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* *Ascyltus pterygodes* was seen to attack a moth whilst in the act of oviposition—Caboni, ix/25.
† *I.e.* whilst the moths are settled on the leaves.

Thus, in field counts made by us and by previous observers,* the average number of eggs per mass has always been less than thirty.

The eggs in each cluster seldom touch each other, although they are grouped close together, and they are laid all facing in the same direction and with their longitudinal axes approximately parallel with each other.

They are somewhat loosely attached to the leaf, and with care they can be brushed off without damage; but attachment is not always by the same surface. Eggs may lie with either dorsal, ventral or a lateral surface uppermost.

Knowles states that the longitudinal axis of the eggs is parallel to the veins of the leaflet; but we have found that this is by no means always the case. In fact, out of a collection of twenty clusters only four were laid with the longitudinal axis parallel to the veins; whereas three had it at right angles and the remaining thirteen were all obliquely disposed. (Plate XXIV, Fig. C, is a photograph of several egg-masses collected from the field.)

The whole egg-mass sometimes takes on a curved form; but usually a moth, whilst ovipositing, progresses in a straight line after laying the first eggs of a batch.

The clusters are composed of a number of more or less regular rows of eggs, but the number of eggs in each row varies. Infertile eggs are often laid in rather scattered groups, the component eggs facing in various directions.

4. Infertile Eggs.—Infertile eggs were of rather rare occurrence in the field during the large outbreaks prior to the introduction of *P. remota*. But since the end of 1925 several records of such eggs have been noted. An opportunity to study them was also presented by our breedings of the moth inside the wire cage in Suva (*vide* preceding table).

Infertile eggs are laid usually either singly or in small clusters of less than twenty: and such clusters frequently display no uniform symmetry of arrangement.

They remain as a rule quite unpigmented and gradually shrivel up, leaving a series of dark spots on the leaf—the residue after fungus attack. Sometimes they are pigmented to a greater or less extent, but, although similar in colour, the pigment can be distinguished from that of the more mature fertile eggs by the fact that it is very irregularly disposed and not in a definite band.

We have seen occasional large egg-masses in which one or two eggs were infertile, but under normal conditions not more than 5 per cent. of the eggs in each brood are infertile, and these are laid in separate masses or singly.

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* "A number of clusters contained from eight to fifty-three eggs averaging twenty."—A. Diespeissis. ". . . they are laid in clusters of twenty to thirty."—H. W. Simmonds.

LARVAE

1. Morphology.—*General Description.*—The larvae * of *Levuana* are slug-like in appearance and beset with tufts of short, stout hairs. When feeding on a leaf, they appear white with two black lines running the length of the body on the upper side. In a close view it will be seen that these lines are really composed of a number of separate segmentally-disposed dark purple spots. In a front view another black mark will be seen on the anterior end of the larva. This mark is the pigment on the cervical shield of the prothorax and is a useful character for distinguishing various species of Zygaenid larvae.

The larva owes its somewhat unusual appearance to the fact that, unlike most caterpillars, the integument is thin and, except on the prothorax, completely lacking in pigment; so that the internal organs show through the transparent skin, and give the larva a white or creamy tint.

When newly hatched, a larva measures not more than one millimetre; when fully grown it is slightly over half an inch long (13 mm.).

The greatest width is rather in front of the centre of the body—at about the second and third abdominal segments. From this point, the body tapers posteriorly to the anal segment, which is only about half as wide.

The head is completely withdrawn beneath the prothorax, except just after a moult or when the larva is crawling about.

In order to gain a conception of those characters of a larva most likely to be of use from the taxonomic viewpoint, we made an examination of the mature larva of six different species of ZYGAENIDAE occurring between Fiji and Malaya. The following characteristics were applicable to all six species, and are very probably typical for all larvae of the family :—

1. Head more or less retracted within the prothorax.
2. Head capsule weakly chitinised posteriorly.
3. Integument thin except on the cervical shield and suranal plate.
4. Integument unpigmented and transparent except on the cervical shield.
5. Prolegs present on abdominal segments 3, 4, 5, 6 and 10.
6. Crotchets arranged in a uniordinal meso-series.
7. Larvae are slug-like in form.
8. Armature of the body consists of a series of rather short, stout bristles arranged in verrucae (except during the first instar).
9. Spiracles small and subcircular; that on the prothorax larger than any others.
10. Presence of an eversible gland on the pleuron of the second and seventh abdominal segments.

Body Armature of Levuana.—One of the most characteristic features of the larva of *Levuana* is its vestiture of stout setae, which forms such a complete covering to the exposed parts of the body that it is almost impossible to touch the integument with a needle without first encountering a seta. As soon as a larva becomes apprised of danger by something touching one of its setae, it will contract itself, and in so doing closes up those articulating parts of the body not covered with setae.

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* See Plates XXIV, XXV and XXX, Fig. 4.

The same general arrangement of setae applies to all stages of larvae, so that it is convenient to describe it here before passing on to an account of the several instars (see Figs. 20 and 21).

Except during the first instar, verrucae containing anything from five to sixty setae are developed on all segments except the prothorax and tenth abdominal. This one applies to the upper surface of the larva ; on the ventral surface, which during feeding is closely applied to the leaf and consequently somewhat flattened, there are no verrucae and only a few single setae.

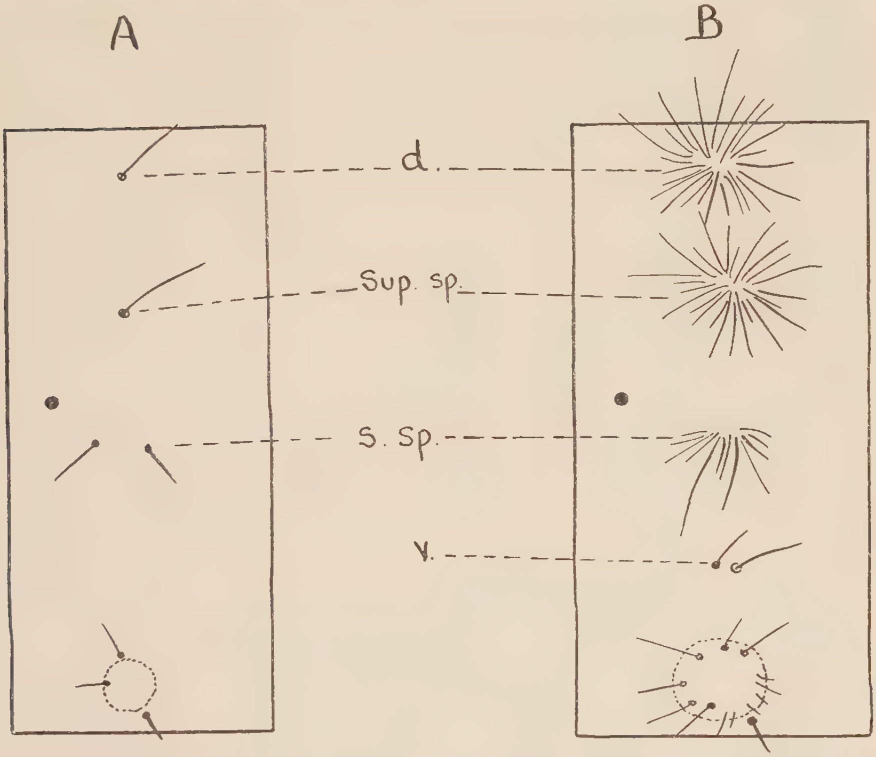

FIG. 20.—Diagram of third abdominal segment of (A) first stage and (B) fifth stage larvae of *Levuana iridescens :* to show arrangement of setae. *d*, dorsal seta and verruca ; *sup.sp.*, supra-spiracular seta and verruca ; *s.sp.*, sub-spiracular seta and verruca ; *v*, ventral setae (not developed into a verruca in *L. iridescens*). The position of the proleg is shown by a dotted line. The spiracle is shown as a black spot occupying a central position in the anterior part of each segment.

There are four verrucae on the meso- and meta-thorax, three on each of abdominal segments 1 to 8, and two on the ninth abdominal segment. These numbers refer, of course, to one side only of each segment.

We have not attempted to apply Fracker's system of nomenclature for the various setae. In order from dorsal to ventral, the verrucae will be named as follows :

Thorax.	Abdomen 1–8.	Abdomen 9.
Dorsal.	Dorsal.	Dorsal.
Supra spiracular.	Supra-spiracular.	
Spiracular.		
Sub-spiracular.	Sub-spiracular.	Ventral.

The number of setae in each verruca varies considerably in different individuals, and often there is a small difference in number between the setae of the corresponding verrucae on either side of the same larva. There is a steady increase in the number of setae in each verruca after each moult, but the numbers for each stage vary within such wide limits that it is not possible to include such numerical data in a scheme for distinguishing the instars.

There are four types of seta found on *Levuana* larvae (Fig. 22, A, B, C, D).

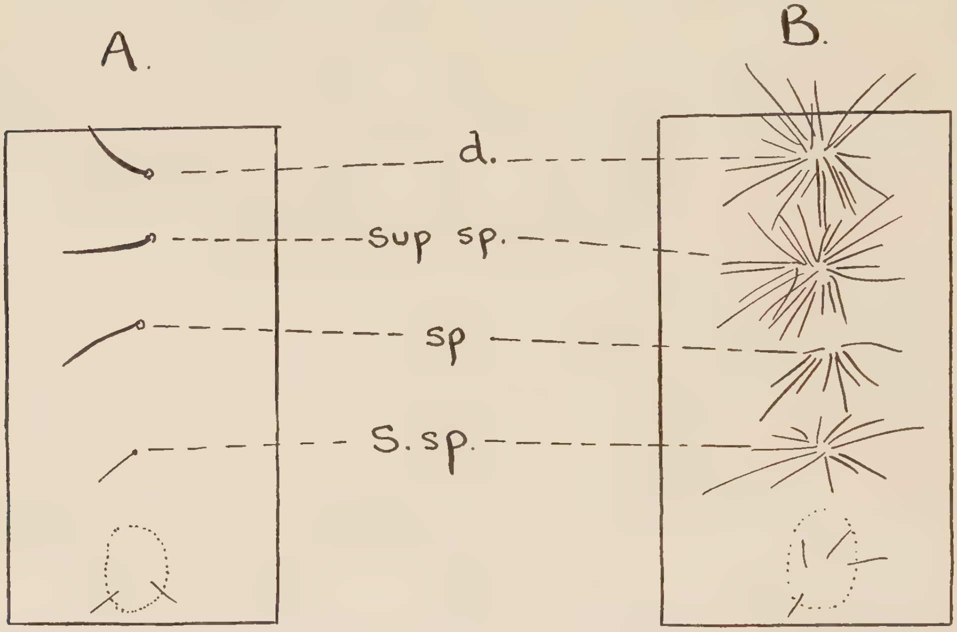

Fig. 21.—Diagram of the metathoracic segment of (A) first stage and (B) fifth stage larvae of *Levuana iridescens* : to show the arrangement of the setae. *d*, dorsal seta and verruca; *sup.sp.*, supra-spiracular seta and verruca; *sp.*, spiracular seta and verruca; *s.sp.*, sub-spiracular seta and verruca. The position of the leg is shown by dotted line.

One type (A) is found in the first instar and is the type of seta of the dorsal and supra-spiracular groups. This is later modified to another type (C) which is found in the dorsal and supra-spiracular tufts of second and third stage larvae. A third type (D), and intermediate forms, replace type C in the corresponding verrucae of fourth and fifth stage larvae. The longer bristles of the supra- and sub-spiracular verrucae right through each stage belong to the type B. The long setae from the ninth abdominal dorsal verruca and the mesothoracic dorsal also belong to type B.

Many of the dorsal setae of the types C and D are pigmented. Setae of type B are never pigmented.

First Instar (Fig. 23).—Length when newly hatched, 1 mm. Maximum length during first stage, 1·8 mm. Verrucae are not developed; setae arise singly from the integument. Subcutaneous pigmentation evident in subrectangular patches on the mesothorax and abdominal segments 1, 2, 3, 4, 5, 6 and 9; the pigment on abdominal segment 3 being rather paler than that on the other segments. The head capsule is 0·28 mm.* wide. The pigment on the cervical shield is undivided and forms a transverse band across the prothorax. It is very constant in shape during this stage (see Fig. 24). A larva after hatching usually eats the whole or a portion of the egg-shell before commencing to feed on leaf tissue.

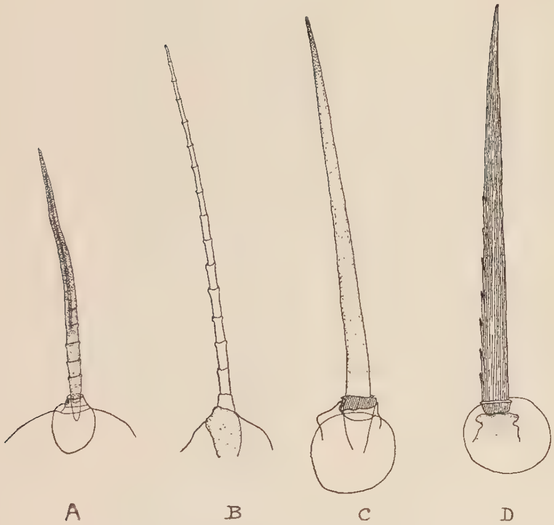

FIG. 22.—*Levuana iridescens*.—Larval setae—four types. A. Dorsal bristle of first instar. B. [Dominant of] ninth abdominal dorsal bristle of first instar. C. Major bristle from dorsal tuft of metathorax of third instar. D. Major bristle of abdominal segments of fourth and fifth instar.

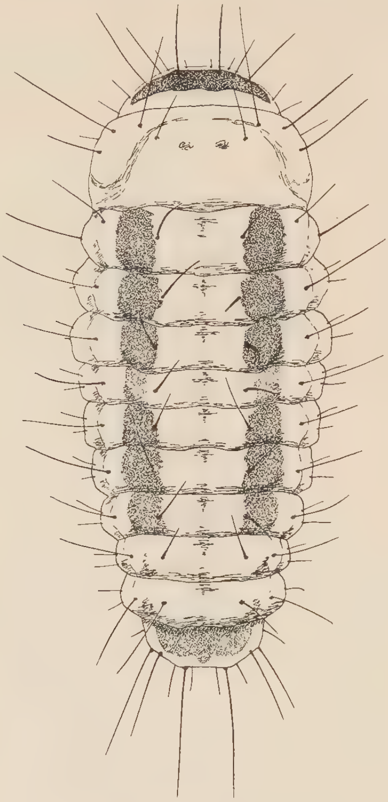

FIG. 23.—*Levuana iridescens*.—First instar larva in position for moulting. ×80.

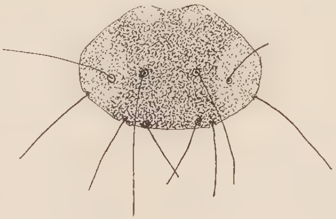

FIG. 24.—*Levuana iridescens*.—Cervical shield of first stage larva. × 90.

Second Instar (Fig. 25).—The maximum length observed was 3·1 mm. Verrucae are developed on those segments and in those positions in which they

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* An average figure for a number of individuals.

occur in the mature larva. There are at most twelve setae in a single verruca (the mesothoracic dorsal). Short, fine setae are lacking on the posterior half of the cervical shield (Fig. 26). The subcutaneous pigmentation is of variable extent. In addition to those segments in which it was developed in the first instar there is often a rather poorly discernible patch on the mesothorax and seventh abdominal segment, while the pigment of the third abdominal segment is now as intense as the rest.

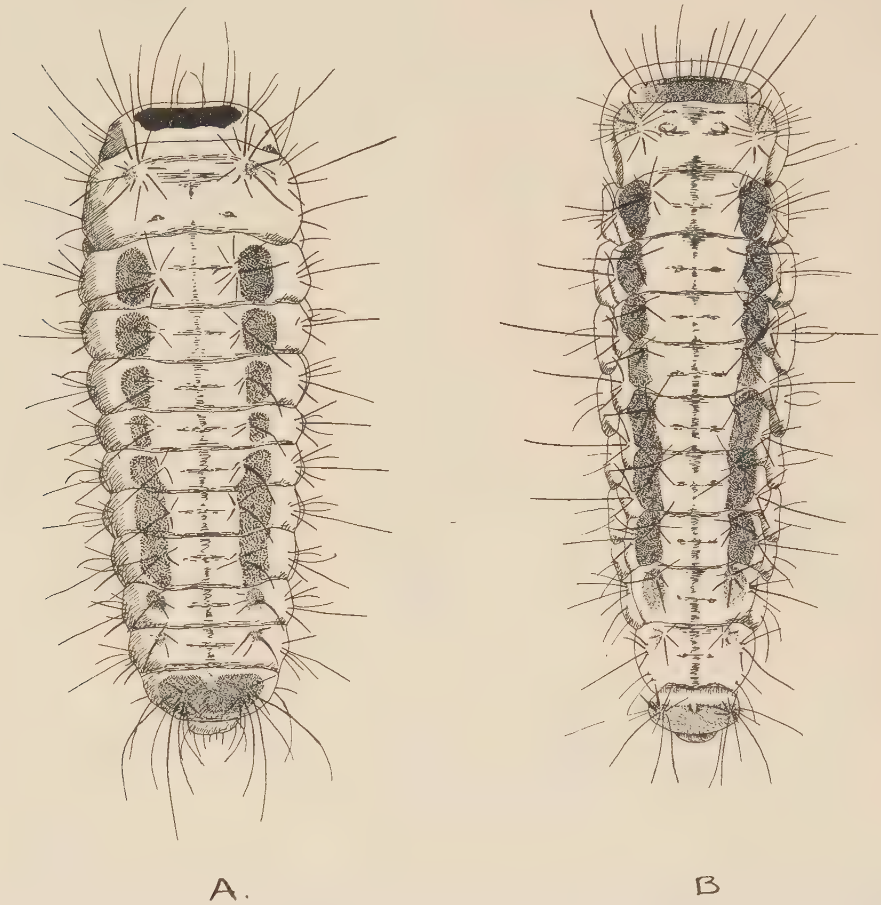

FIG. 25.—*Levuana iridescens.*—Second instar larva, dorsal view. A. In position for moult, × 57; B, in feeding position, × 50.

The cervical shield pigment is still undivided: the lateral margins are somewhat indistinct, but the main area of pigment is approximately square, or if anything longer in an antero-posterior direction. It is also slightly notched posteriorly (see Fig. 26).

The head capsule is 0·40 mm.* wide.

Third Instar (Fig. 27).—Maximum observed length, 5·5 mm. At least two pairs of short fine setae are present on the posterior half of the cervical shield (see Fig. 28). This readily separates third from second instar larvae.

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* Average for several individuals.

Dorsal verruca of mesothorax containing about eighteen to twenty setae. Dorsal verrucae of abdominal segments 1–8 each containing from five to twelve setae.

The subcutaneous pigmentation becomes almost complete during this instar, *i.e.* developed on all segments from the mesothorax to ninth abdominal inclusive. But there is much variety in this respect, and the pigmentation on the eighth abdominal segment (the last to develop) is often wanting until the completion of the third moult.

The cervical shield pigment is very variable during this stage. It is often incompletely divided by a narrow median split from the posterior margin. The lateral margins are sometimes clearly defined. In other individuals there is much suffuse pigment at the edges of the main area. A typical condition is shown in our figure (Fig. 28).

The head capsule averages 0·55 mm. in width.

Fourth Instar (Fig. 29).—Maximum observed length 6·9 mm. The dorsal verruca of the mesothorax contains about forty setae, that of the metathorax about thirty setae, and those of the first eight abdominal segments about twelve setae.

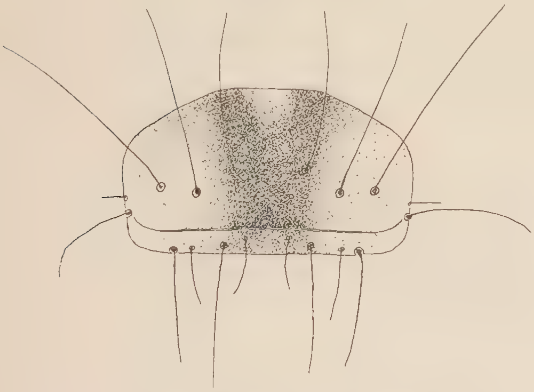

FIG. 26.—*Levuana iridescens.*—Cervical shield of second-stage larva. × 90.

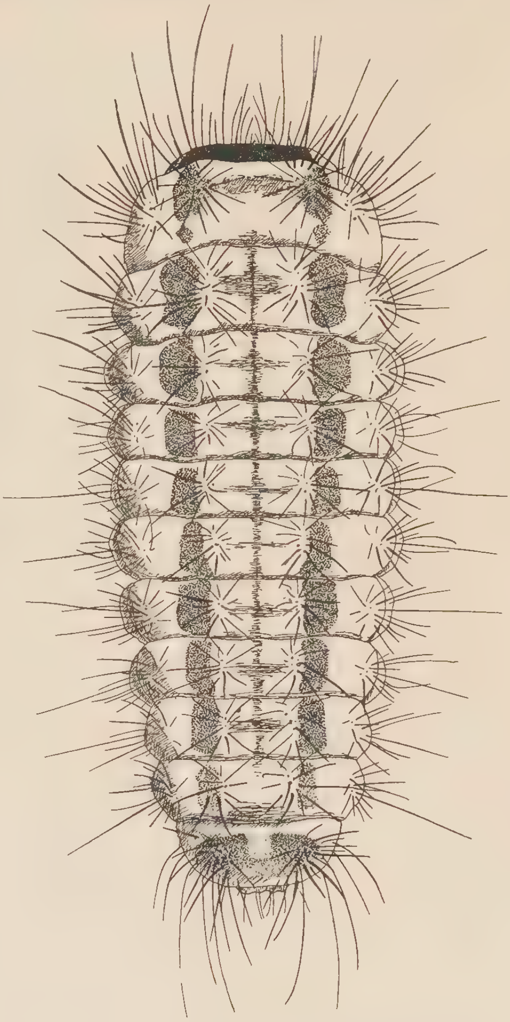

FIG. 27.—*Levuana iridescens.*—Third-stage larva in moulting position. × 40.

The subcutaneous pigmentation is complete after the third ecdysis, *i.e.* pigmented areas are present on every segment from the mesothorax to the ninth abdominal (inclusive).

The gonads of the male sex can sometimes be distinguished during this instar. They show through the dorsal integument of abdominal segments 4 and 5 as opaque white lobes. The ovaries are inconspicuous.

The pigment on the cervical shield (Fig. 30) is completely divided medially into two parts. The intervening unpigmented part is often very narrow, and the dual nature of the pigment can then scarcely be distinguished without magnification. The pigment extends on to the anterior sixth of the shield.

The head capsule averages 0·76 mm.

Fifth Instar (Figs. 31 and 32).—This is the final larval instar, and we give a fuller description than was necessary for the earlier stages. Maximum length 13 mm. Maximum width 3 mm. at second abdominal segment.

Head.—Completely retracted with the prothorax, posterior part feebly chitinised. Adfrontals indistinct, no adfrontal setae (Fig. 33). Epicranial sutures meet at one-third the distance from the base of the mandibles to the vertical margin. Only five ocelli fully developed; the sixth (No. 1 of Fracker) is rudimentary; the arrangement of the ocelli is as shown in Fig. 34, C. The antenna and mandibles are not remarkable (Fig. 34, A, B). The labrum (Fig. 34, D) is notched medially on the anterior edge, the arrangement of setae being shown in the figure.

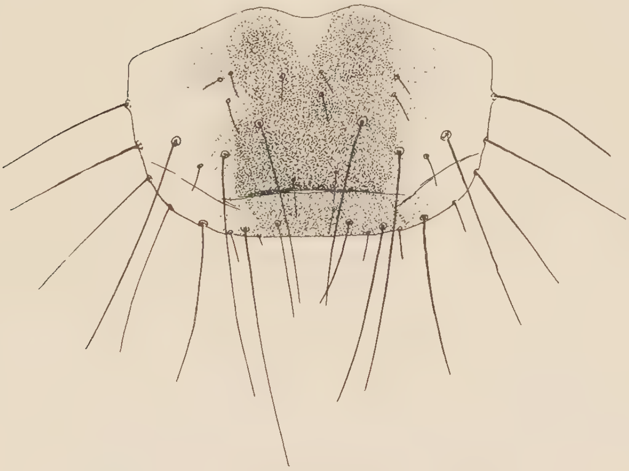

FIG. 28.—*Levuana iridescens.*—Cervical shield of third-instar larva. × 90.

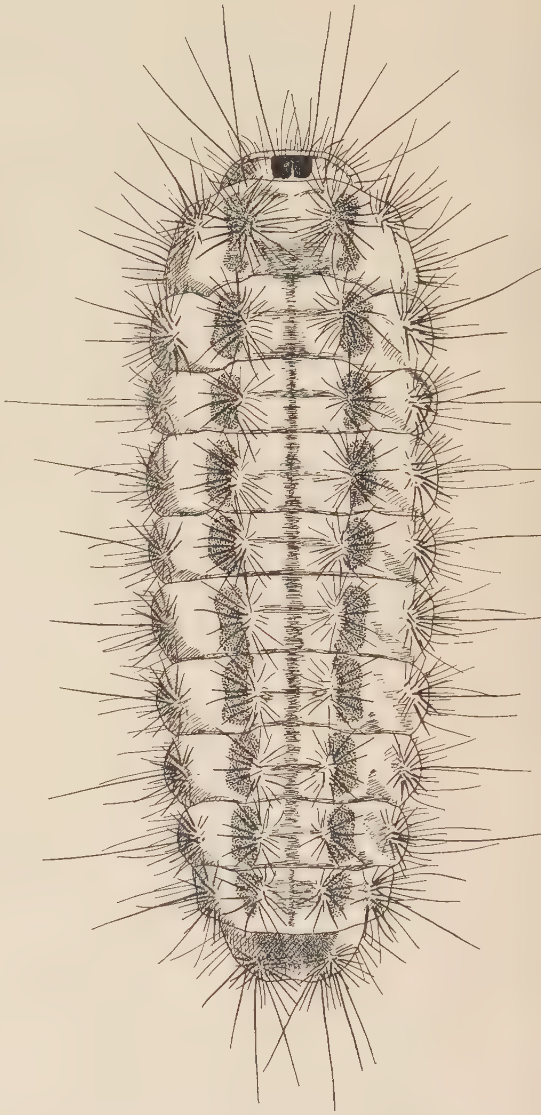

FIG. 29.—*Levuana iridescens.*—Fourth-instar larva in moulting position. × 26.

Prothorax.—The cervical shield is bounded anteriorly by the feebly chitinised anterior part of the pronotum devoid of setae (Fig. 31, *a*). This fleshy part of the segment is apposed to the leaf in the manner of a sucker when the larva feeds. The cervical shield (Fig. 35) is beset with numerous fine setae which vary in position on different individuals. In addition to these, there are eight long setae which are constant in position and project forwards and downwards, round the anterior end of the larva. The shield pigment is clearly separated down the median line into two lozenge-shaped patches, which extend from nearly the post limit of the segment for five-sixths of the distance to the anterior margin of the shield. The anterior sixth of the shield is either very feebly pigmented medially or lacking in pigment altogether. The spiracle is shown in Fig. 36.

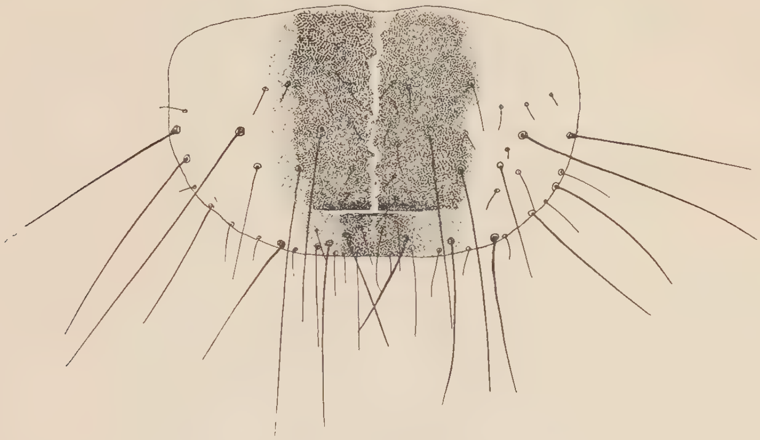

FIG. 30.—*Levuana iridescens.*—Cervical shield of fourth-instar larva. × 80.

Mesothorax.—The dorsal verruca contains forty to fifty setae, two or three of which are nearly twice as long as the rest and project forwards above the pronotum. These long setae are of the type figured at B, Fig. 22. Supra-spiracular verruca with about the same number of setae as the dorsal, two of which are twice as long as the rest. The other verrucae on this segment contain a smaller number of fine setae arranged more nearly in a longitudinal row and varying in length. The subcutaneous pigment on the mesothorax forms a dumb-bell-shaped figure, the anterior portion of which is beneath part of the dorsal verruca.

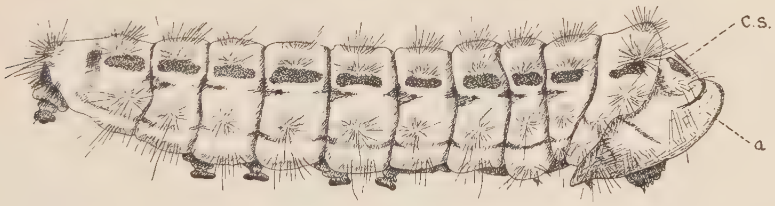

FIG. 31.—*Levuana iridescens.*—Lateral aspect of fifth-stage larva to show extension of prothorax to form a hood-like covering to the head. × 20. *c.s.*, cervical shield; *a*, anterior feebly chitinised and asetiferous part of pronotum.

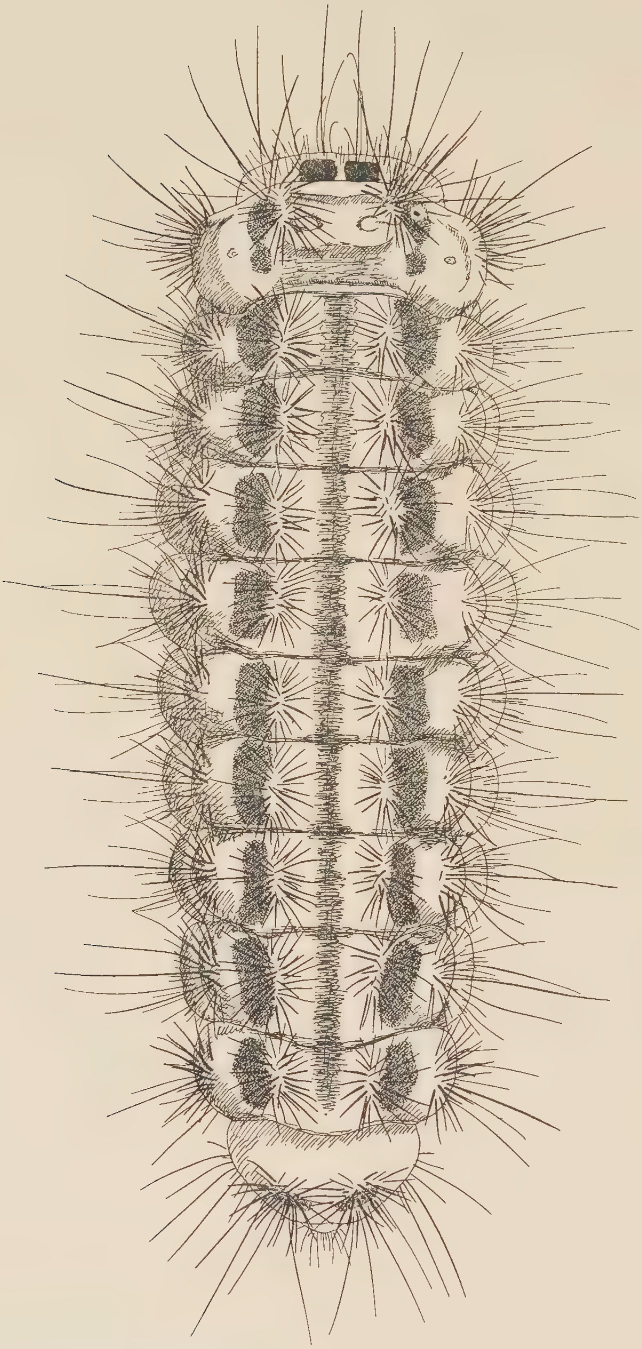

FIG. 32.—*Levuana iridescens.*—Fifth-instar larva, dorsal view (killed in chloroform). × 25.

Metathorax.—The dorsal verruca with somewhat fewer setae than that of the mesothorax, all of approximately even length. The supra-spiracular verruca contains a similar number of setae, one of which is at least twice as long as the rest and projects slightly downwards and outwards from the segment. Spiracular and sub-spiracular verrucae as in mesothorax. Subcutaneous pigment in a rectangular figure just laterad of the dorsal verruca.

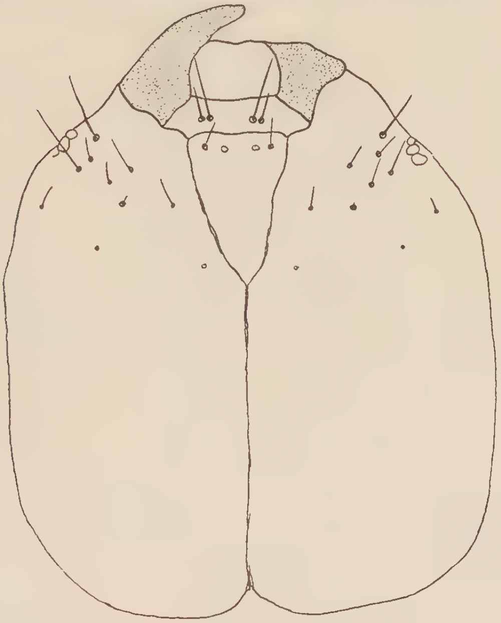

FIG. 33.—*Levuana iridescens.*—Dorsal view of head capsule of fifth-stage larva to show epicranial, frontal and clypeal setae. Setae of labrum omitted. × 100.

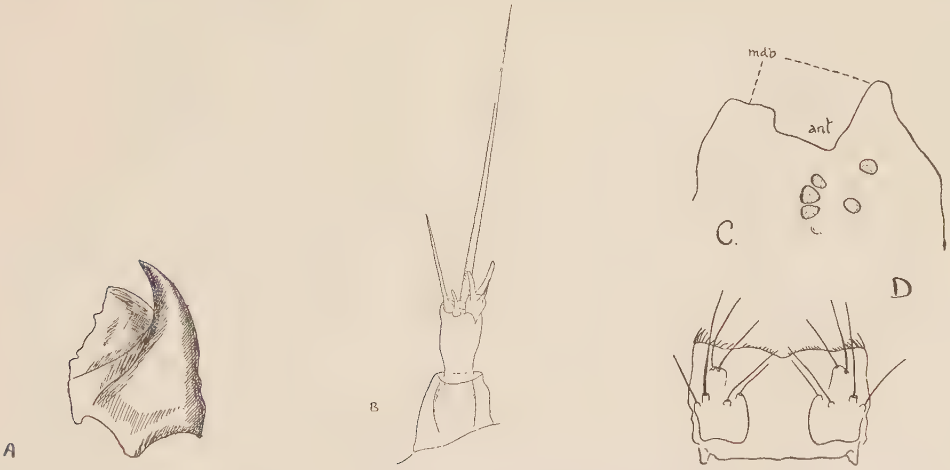

FIG. 34.—*Levuana iridescens.*—A. Mandible—dorsal aspect. B. Antenna of left side—dorsal aspect. D. Labrum—dorsal aspect. All much enlarged. C. Part of epicranium on right side to show arrangement of ocelli, one of which is vestigial; *ant.*, insertion of antenna; *mdb.*, articulating surface of mandible.

Abdominal Segments 1 *to* 8.—Dorsal verrucae with twenty-five to thirty-five stout setae of about equal length, many of them are the type shown at D in Fig. 22. Supra-spiracular verrucae each with fifteen to thirty setae one or two of which are nearly twice as long as the rest. Sub-spiracular verrucae forming a longitudinal fringe of ten to fifteen rather fine setae of varying lengths.

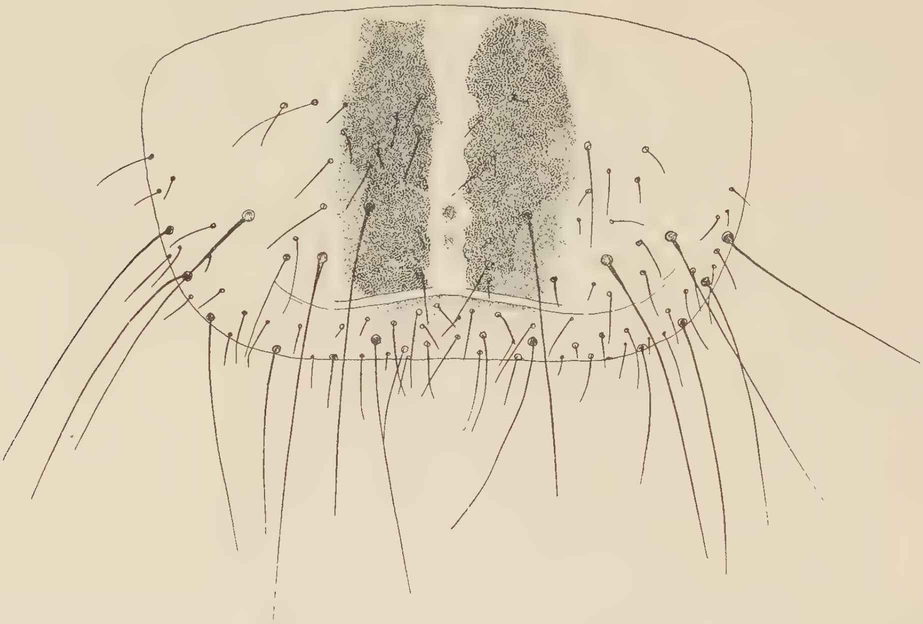

Fig. 35.—*Levuana iridescens.*—Cervical shield of fifth-instar larva. × 80.

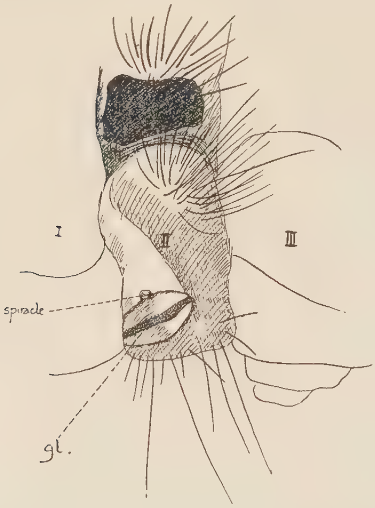

Fig. 36.—*Levuana iridescens.*—Lateral aspect of second abdominal segment of fifth-stage larva to show spiracle and gland (*gl.*).

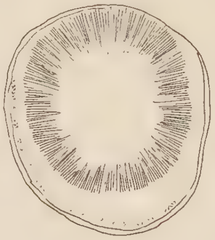

Fig. 37.—*Levuana iridescens.*—Prothoracic spiracle of fifth-stage larva.

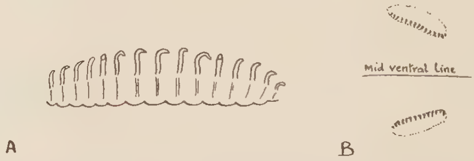

Fig. 38.—*Levuana iridescens.*—A. Crochets on sixth abdominal segment proleg of fifth-instar larva. B. Diagram to show distribution of crochets around the planta.

Subcutaneous pigment in each segment much as in metathorax. On segments 2 and 7 opening just ventrad of the spiracle is a semi-eversible gland of unknown function (Fig. 36, *gl.*). The gland is elliptical in outline, divided by a horizontal slit into two "lips" which can be opened and closed. These glands become conspicuous in certain larvae after prolonged immersion in alcohol, but in a living specimen they are rather difficult to see. They are present on the same segments of all the Zygaenid larvae we have seen. They are first visible in the embryo a few days before hatching and persist throughout the immature stages.

The crotchets (Fig. 38) are in a uniordinal meso-series, their length decreasing from the centre outwards.

Abdominal Segment 9.—Dorsal verruca with about thirty to forty setae, four of which are quite twice as long as the rest and project in a posterior direction. The ventral verruca contains about twelve fine setae of varying length.

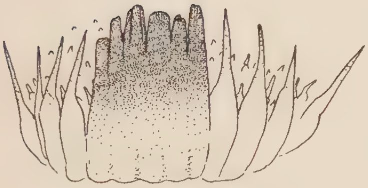

FIG. 39.—*Levuana iridescens.*—Anal "comb" of mature larva. Much enlarged.

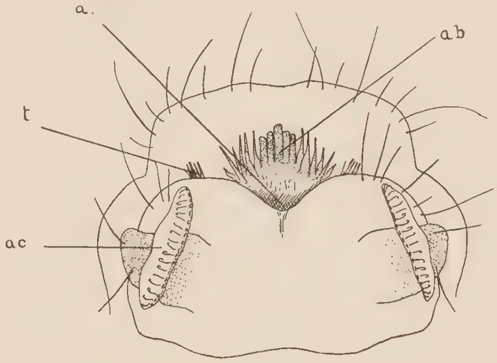

FIG. 40.—*Levuana iridescens.*—Diagram of posterior view of anal segment of fifth-instar larva, to show position of anal "comb" (*a.b.*), anus (*a*), ventral paired tufts (*t*), and anal claspers (*a.c.*).

Abdominal Segment 10.—The suranal plate is beset with small spines, and has distally a row of stiff, rather flattened processes placed side by side like the teeth of a comb: the processes decrease in length from the centre outwards.* This "anal comb" is present on all stages of larvae and aids in the ejection of the faecal pellets. There is a small tuft of stiff processes on either side of the anus ventrally (Fig. 40, *t*). Verrucae are not developed on this segment.

2. Note on the Preservation of Larvae.—The subcutaneous pigment of the larva of *Levuana iridescens* is destroyed by all the usual preservatives, and we have not yet been able to discover any method of preserving the natural colours of larvae.

The cuticular pigment on the cervical shield is only slightly affected by prolonged immersion in 10 per cent. KOH, and the usual preservatives have no effect on it.

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* This is variable.

We have kept larvae in 70 per cent. alcohol, 5 per cent. chloral hydrate and weak formalin; and until a method is discovered for preserving the deep-seated dorsal pigment, we recommend alcohol as the best preserving agent.

3. Note on the Separation of the Larval Instars.—We have prepared a field key that may serve to separate the five larval stages of *Levuana iridescens.* The characters of successive instars for each individual larva are always quite distinctive; but the difficulty in producing a key lies in the fact that there are always a number of individuals in any collection of larvae which are so far in arrear of what might be claimed as the average condition for any instar, that they display features to some extent intermediate between the typical for their particular instar and the next earlier one.

We had hoped that some absolute distinction might be found in the matter of chaetotaxy; but although this is useful for distinguishing certain instars, it cannot be applied throughout successfully; so we have had to fall back on such characters as colour change which are often apt to be misleading.

Key for Determination of Larval Instars of Levuana iridescens.

1. Pigment on prothorax all in one piece 3
2. Pigment on prothorax divided longitudinally into two more or less distinct and equal parts 7
    3. Verrucae not developed; prothoracic pigment distinctly longer in the transverse direction . . . . . . Instar I
    4. Verrucae present, containing at least five setae; prothoracic pigmentation forming approximately a square or else longer in the antero-posterior direction 5
        5. No short fine setae on the posterior half of the cervical shield; subcutaneous dorsal pigment spots lacking on abdominal eight . . . . Instar II
        6. At least two pairs of short fine setae on the posterior half of the cervical shield . . . . . . Instar III
7. Split between prothoracic pigment areas narrow (often indistinct) and of even width throughout. Distinct pigment on the anterior one-fifth of cervical shield . . . . Instar IV
8. Split between prothoracic pigment areas distinct and wider; usually narrowest in the centre and gaping at either end. Pigment on anterior one-fifth of cervical shield indistinct or lacking . . . Instar V

4. Habits and Behaviour of Levuana Larvae.—On the coconut palm, which is the professed food-plant, the larvae generally feed upon the wider surface of the leaves. The prothorax forms a hood over the head and is apposed to the surface of the leaf during feeding, so that the head is completely hidden from view. A larva when commencing to feed usually takes up a position parallel to the course of the veins of the leaf and starts eating away the surface tissues in a straight line, leaving a characteristic parallel-sided feeding scar, approximately the width of its body. Thus the width of the feeding scars varies as larvae grow; but no reliance can be placed on the feeding scars as an absolute determination of the size of the larva that made them. For instance, a fifth-stage larva was observed to make two feeding scars—one 2 mm. wide, the other only 1·25 mm. wide—during the course of a day's feeding.

The feeding scars of newly hatched larvae are, however, quite characteristic, for besides being short and close together on the leaf, they do not penetrate completely through the parenchyma, as do all those scars left by the feeding of older larvae.

Feeding scars are sometimes a useful rough guide in the field for determining the stage in the life-cycle at which an outbreak terminated.

Feeding scars may attain a considerable length—the longest one noted by us being 8·3 in. long. In a leaf which has already been much defoliated the scars tend to be shorter, since a larva often gets interrupted in its forward progress by meeting another feeding scar, whereupon it will move off to another part of the leaf. Furthermore, if the leaf is withered or otherwise unsuited for food (which frequently happens when cut leaves are fed to larvae in the laboratory), a larva will make several attempts to feed, forming a number of short scars.

Whereas larvae of *Artona catoxantha* during their final instar feed at the edge of the leaf, eating away the entire lamina, larvae of *Levuana* never do this, but feed during all stages on the surface of the lamina.

Levuana larvae are comparatively slow feeders, but feed continuously, unless disturbed, during the daylight hours. Feeding at night has often been observed with larvae kept in the laboratory, but under natural conditions they generally remain motionless during the night either on the last feeding scar or else in the basal angle of the leaflet, assuming an attitude similar to that which precedes a moult. Their feeding activities are resumed with the renewal of daylight. It has frequently been noticed, more especially when larvae are kept in a confined space, that coconut leaf on which *Levuana* is feeding has a characteristic, rather sweet odour. It is not very strong, but three out of four people consulted were able to detect by the odour the difference between unattacked leaves and those on which larvae were at the time feeding. This odour can only be detected when larvae are actually feeding on a leaf; for when they are kept in a glass jar hardly a trace of the smell is discernible; nor is it possible to detect it on a leaf for more than a few hours after all the larvae have been removed.

It was thought at first that this odour was caused by *Levuana* itself, since coconut leaf newly eaten by *Agonoxena* or else crushed in the hand produced none of the odour; but recently in the Solomons it was noticed that freshly opened leaves containing larvae of *Brontispa froggatti* had the same odour as that associated with *Levuana*. It must therefore be due to some specific character of the food plant rather than the insect which is eating it.

On the other hand, there are two rather remarkable facts concerning *Levuana* larvae which seem inexplicable unless we presuppose that such larvae have some specific odour. We refer firstly to the decided preference shown by moths about to oviposit for those leaves on which larvae are actually feeding; secondly to the truly astonishing way in which *Ptychomyia remota* seems able to discover the sudden presence of a few *Levuana* larvae in a locality where none have existed for a considerable period. The following instances illustrate these points.

During 1925 and 1926 we frequently loaded small coconut palms for experimental purposes with egg-masses collected from afar; and in Suva on several occasions we were surprised to find a few days later that moths had flown down from neighbouring high trees and oviposited on those leaves on which larvae, hatched from our eggs, were feeding, while other leaves on the same palms were not visited by the moths.

The remarkable ability of the Tachinid parasite to detect *Levuana* was well illustrated by an experiment which was conducted on Naigani in September, 1927. About 110 larvae at various stages of development were placed on a leaf of a small coconut tree in the centre of the island. The leaf was ringed at the base with a broad band of tanglefoot, and all surrounding vegetation likely to touch the leaf removed. At this time there had been no trace of *Levuana* on the island for nearly eighteen months.

The locality was revisited fourteen days after the larvae were put out. Some had crawled into the tanglefoot when moving off the leaf to pupate ; the youngest on the leaf being fourth instar. They were all collected, and 84 per cent. were found to be parasitised by the fly, many having more than one parasite egg laid on them.

An attempt was therefore made to isolate from *Levuana* larvae some body that had a perceptible odour when concentrated. Four grammes of larvae were placed in a small distilling flask connected to a vacuum pump. The receiver was kept in ice and salt at approximately 10° C. The distilling flask was gently heated in a water-bath to 50° C. A quantity estimated at 1·0 c.c. of clear liquid was obtained having a somewhat musk-like odour. The liquid contained an unsaturated organic compound, but no identification was possible. Some of the liquid was smeared on a coconut leaf which was left with a female moth in a jar. The moth died without ovipositing, and the odour soon dissipated. Unfortunately it was not possible to conduct a field experiment with the fluid owing to the scarcity of the moth at the time.

When the food supply becomes exhausted, as often happens after five or six broods have fed continuously on the same tree, larvae do not crawl away on to neighbouring trees, but crawl all over the defoliated tree and, when finally unable to discover any food, suspend themselves on threads of silk and eventually perish amongst the débris at the base of the tree unless sufficiently mature to pupate.

In a bad outbreak it was no uncommon sight to see dozens of larvae hanging on threads of silk from the leaves, and we found that a similar behaviour often took place when arsenical sprays had been applied to the leaves on which they were feeding.

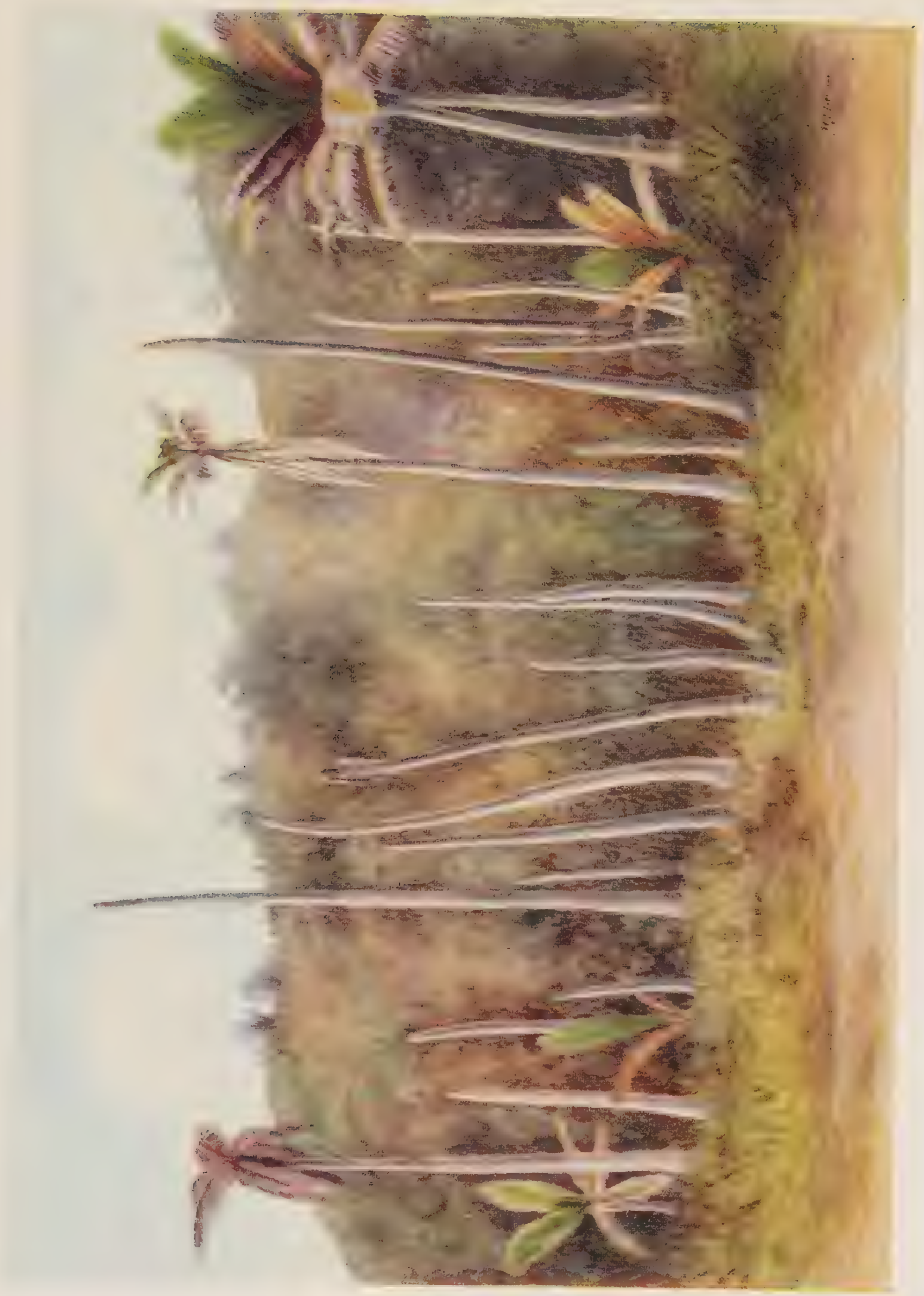
The larvae of *Levuana* are unable to find their way on to a coconut tree when once they reach the ground. Some sixty larvae of various ages were scattered over the ground at a distance of not more than 10 ft. from a coconut tree the trunk of which was ringed with tanglefoot 3 ft. above the ground. The surface of the ground round the foot of the tree was in this case covered with closely mown grass. The tanglefoot was examined each day subsequently, and after ten days, not a single larva had succeeded in reaching it. There were no other coconut trees within a distance of 80 ft., so it was almost certain in this case that the larvae perished. Furthermore, the

PLATE IV

THE DEATH OF TREES CAUSED BY *LEVUANA*

Sometimes two and sometimes three successive outbreaks of *Levuana* resulted in the death of trees. Actual mortality of this kind was seen on Ovalau, Naigani, and Moturiki, but was generally confined to trees living in poorer situations.

PLATE IV



behaviour of larvae when kept in captivity affords further evidence of this inability to find the food-plant, which is in striking contrast to the larval habit of *A. catoxantha*. Larvae of the latter species managed to find their way back to the food-plant after crawling over the floor and walls of a cage ; *Levuana* has never managed to do this.

Larvae removed from their food-plant are guided apparently by a phototropic impulse, and in breeding cages they eventually make their way to the main source of illumination irrespective of the location of their food. Larvae will also crawl out of a glass tube towards the light.

This inability to migrate from tree to tree in the larval stage is undoubtedly one of the factors that brings about the enormously rapid decimation of numbers at the end of a large outbreak.

It was considered possible that larvae exhibited a distaste for certain varieties of coconut palm, or for leaves which, having been defoliated during a long period, had become partially dried up. This is a matter rather difficult of absolute proof, for whereas larvae fail to feed for no obvious reason on certain leaves, recent feeding scars have often been observed on what appear to be most unattractive leaves, yellow and fungus-ridden, after the supply of fresher foliage has been exhausted.

Simmonds, in 1921, brought into Fiji from Tahiti some nuts of a variety of palm known locally as the " Oviri," and known to possess astringent properties, but the leaves of these were not distasteful to half-grown larvae which fed on them " for a few days freely." It thus seems unlikely that the unwillingness of larvae to feed on certain leaves is due to the specific character of any leaf rather than some quite unconnected physical factor.

It has been stated above that larvae are phototropic. This impulse is, however, overcome by their objection to the continued action of the direct rays of the sun. When feeding on a tree, larvae, including newly hatched ones, seem quite insensitive to direct sunlight ; but then there is generally sufficient breeze during the hotter hours of the day to keep leaves intermittently shaded, so that in the field sunlight does not seem to play any direct part in limiting the available feeding space. If, however, that part of the leaf on which larvae are feeding is held for a few minutes in full sunlight, the larvae will start to crawl rapidly away into the shade. Five minutes' subjection to the direct rays of the sun does not harm the larvae ; but when the rays strike them through glass, they will die in a comparatively short time.

When ready to moult, larvae usually crawl into the sheltered basal angle of the leaflets, although they sometimes moult on the more exposed part of the leaf or lie along the midrib of the leaflet. The basal angle of each leaflet is usually crowded with moulting larvae when the infestation is heavy and their moult skins remain for months attached to the leaf in that position, long after the bulk of the leaf has withered and fallen away.

A few threads of silk are spun on the leaf, and the larva anchors itself to this platform with the anal prolegs. The larva then contracts somewhat in length and remains motionless in this position, until the old skin splits and the larva crawls out, leaving the old skin heaped up behind it on the web. After ecdysis there is generally a resting period for a few hours with the head fully extended and raised slightly above the body. In this position the new integument dries and hardens. The head is then withdrawn into the prothorax, and after a further prolonged rest, the larva resumes its feeding activities. The resting period antecedent to the moult is usually one and a half to two days, and larvae do not as a rule start to feed until six hours after the moult has taken place. When larvae are removed from the silken platform less than a day before they are ready to moult, they are unable to construct another web and experience considerable difficulty in extricating themselves from the old skin.

The characteristic attitude of larvae ready to moult is well shown in Plate XXVI, Fig. E.

Larvae are unable to move rapidly, crawling being a very deliberate process. Their only mode of defence is to withdraw the head and contract their body segments, thus presenting a completely bristle-covered surface to any would-be enemy. Sometimes, when disturbed, they curl up in the manner of a wood-louse, more especially when just preparing to moult. They do not crawl rapidly backwards or fall from the food-plant on a thread of silk when disturbed.

Inclement weather conditions seem to have very little effect on larvae. In their usual habitat, the under side of coconut leaves, they are protected to a large extent from rain.

The faecal pellets are ejected to a considerable distance by means of the peculiar armature of the suranal plate. There is a comb-like row of flat chitinous processes projecting above the anus ; at defaecation the rectum is evaginated with the faecal pellet and the latter is grasped by the comb and hurled out behind.

5. Larvae with more than the Normal Number of Instars.—The occurrence of extra larval instars has already been discussed from the point of view of duration of development. It was also pointed out that, although the intercalation of extra ecdyses makes it impossible to frame any single key which would hold good for all individuals, the larvae which undergo this abnormal, or rather atypical, development do not display any unique and at the same time constant morphological features. The first instar in every case is normal, and the final instar prior to pupation is also always distinguishable by the arrangement of the pigment on the prothoracic shield. Divergence from the typical seems to start, after one of the intermediate moults, by a larva assuming characters which are intermediate between the instar it has just concluded and that to which it would normally have changed. After this the lagging behind continues during the subsequent stages until finally remedied by the intercalation of one extra moult, after which the larva assumes the characters typical of the normal fifth stage. There is absolutely no doubt at all that such abnormalities did occur, however unlikely it may seem, because after the first occurrence another series of breedings were carried out with the utmost care and the same phenomenon was observed. The time was not at our disposal to make an exhaustive study of the phenomenon, but it seems sufficiently interesting to place on record as far as it goes.

6. Abnormalities.—*Albino Strain of Levuana.*—On a small tree plentifully loaded with all stages of *Levuana* larvae in the centre of an extensive outbreak were found a few fourth- and fifth-stage larvae completely lacking the usual dorsal subcutaneous pigment.

Nine of such larvae were reared. The resulting pupae were also devoid of the pigment ; but the adults developed perfectly normally and were fully pigmented. It is probable that all the " albino " larvae hatched from the same egg-mass, since they were feeding on the same leaf. No other such larvae were ever seen.

Skin Affection.—Larvae have occasionally been found with parts of the skin—on the dorsal and dorso-lateral surfaces only—appearing as if smeared in patches with shellac. Such affections may occur on any segment of the body. Although such larvae appear pathological, they have in all cases recovered their normal condition after the subsequent moult. Most of the observed cases were larvae collected from the field ; but in one instance a larva, whose development from the egg was being studied, contracted the skin " disease " two days after the third moult. The affection remained during the fourth instar, but was moulted off with the skin at the fourth ecdysis, after which the larva appeared perfectly normal.

The symptoms suggested bleeding, since the blood of many insects becomes pigmented on exposure to the air ; but usually bleeding, if induced by a slight abrasion of the skin, causes rapid death of the larva ; so in this instance, if bleeding was the cause it was evidently attributable to some internal factor.

THE PREPUPAL STAGE

The first sign of the fifth-stage larva becoming prepupal is a slight reddening of the anterior abdominal segments. The larva also becomes sluggish and finally ceases feeding. During the ensuing resting period, of about six hours, usually spent on the leaf, the larva gradually becomes reddened internally and assumes a colour which is readily distinguishable from that of other fifth-stage larvae still in the feeding stage. There is an accompanying contraction in length as the colour changes. After this resting period, the larva begins actively to crawl about in search of a suitable place in which to spin its cocoon. It is now no longer influenced by phototropism, but crawls down the leaf on which it has been feeding into the shaded cracks at the base of the leaves and fibre. The most favoured situation for pupation on a coconut tree is in the crack formed between the base of the petiole of one leaf and the fibrous stipule of the succeeding leaf. Larvae usually crawl right down into this crack, succeeding generations going lower and lower down as the crack gradually widens by the downward movement of the maturing leaf.

A percentage of the cocoons is generally made on the leaflets themselves and in almost any other sheltered crevice on the tree, but the great majority of larvae pupate in the fibre or right down on the base of the leaves, and this habit affords an interesting contrast to that of *Artona catoxantha*, which almost invariably pupates on the leaflets.

That photophobism is the impelling force manifest at this stage of development can be shown by keeping prepupae between two watch-glasses exposed to a strong light. Under such conditions the prepupae are very unwilling to start cocoon-making and crawl round and round the container in their efforts to escape from the light. Remove the source of light, and cocoon-making will soon begin, only to be abandoned again when the light is renewed.

Another curious feature displayed by prepupal *Levuana* is a gregarious instinct. It is quite remarkable how cocoons will be constructed *en masse* over a very limited space rather than separately over a wider area. That this is due partly at any rate to gregariousness was shown when larvae were reared in large glass specimen jars evenly illuminated on all sides. The last to pupate almost always constructed its cocoon against one of those previously formed, although abundant unoccupied situations were still available. There is nothing in the habits or structure of the pupa to suggest that anything but harm can result from this habit of massing together cocoons; and it is unquestionably one of the principal factors in the control of the moth at the concluding stages of an outbreak. The masses of white cocoons on the "vulu" (a convenient native word for the fibrous leaf stipules of the coconut tree) and leaf bases are a very characteristic and conspicuous feature of trees infested by the moth; and it was one of the first things sought for during an inspection of a suspected area.

With larvae kept in captivity, the first signs of the prepupal stage were usually noticeable during the forenoon. By evening the prepupae would have finished constructing the basal platform of the cocoon. During the night the remainder of the cocoon was completed; but the final lining to the cocoon takes some time to complete, and prepupae seldom crawled back on to the base of the cocoon until quite twenty-four hours after the commencement of spinning operations.

The manner of spinning the cocoon is as follows: A fine covering of silken threads is woven over a small elliptical area of the surface selected for pupation. This forms the basal platform of the cocoon and is composed entirely of secretion from the silk glands. It is analogous in its function to the silk platform constructed beneath a larva during ecdysis, serving as an anchorage for the fifth instar moult skin. The construction of the basal platform takes about an hour. Then the prepupa begins to spin the covering lid of the cocoon by looping threads of silk round the hair tufts of the fifth and sixth abdominal segments and anchoring the ends on the outer edge of the anterior part of the basal platform. This process is continued on each side for about half an hour; at the end of which time a light web has been constructed over all the anterior half of the larva except for a small circular area immediately above the head, which is inaccessible to the larva while in this position. The threads of each side are then anchored together mid-dorsally, and the larva is able to free its setae from their supporting function and turns round so as to face the opposite end of the cocoon. This end (the posterior) of the lid is now spun up in the same manner; so that after two hours of cocoon-making the structure consists of a completed basal platform and a fine superstructure consisting entirely of silk threads with a small circular breach at each end. At this stage the larva turns on its back and crawls on to the under side of the lid. The two gaps at the ends of the lid are now covered in. Hitherto the entire structure is made from silk gland secretion ; but at this stage another substance is brought into use. As the last breach is covered the larva begins to turn round, and in so doing applies the anus to the central part of the lid at the anterior end. A large drop of milky fluid is then ejected from the anus on to the under side of the cocoon lid. This fluid can be observed in the rectum prior to ejection through the anus ; but its exact chemical nature was not ascertained, and it is not known what organ secretes it. It reacts to the same chemical tests as the secretion of the salivary (silk) glands* and is probably one of the fibroin type of substances.

The larva turns round, places its head in the fluid and proceeds to smear it over the anterior end of the cocoon, leaving only a small untreated margin along the base of the lid. The head of the larva is then pressed right up against the centre of the newly smeared area, and in this position the larva remains motionless for about two minutes, at the end of which time the anal fluid has dried in the form of fine white fibrous crystals. It is this secretion from the anus which forms the opaque papery substance typical of the cocoons of Zygaenids, Taylor being the first to note this phenomenon in a species of *Artona* in Java.

The anterior end of the cocoon is then reinforced with further silk strands beneath ; and then a second drop of anal fluid is exuded at the other end and the process repeated.

The cocoon is finished off by removing pieces of the opaque substance from places where it is thick to other places not covered with it in the first instance, and the inside is finally covered over with a lining of silk. The lid is less securely fastened anteriorly, and this affords an easy exit for the pupa when mature.

When completed, the cocoon lid is opaque so that the development of the enclosed insect can be studied only by removing the top of the cocoon. This can be done without danger of destroying the pupa or prepupa, if reasonable care be taken. The completed cocoon measures 5 by 10 mm.

After completing the cocoon, the prepupa lies motionless on the basal platform for about two days before ecdysis occurs, during which time a gradual change in form takes place. First of all there is a considerable contraction in length accompanied by increase in width. For the first day the prepupa is more or less larviform and will roll up when disturbed in the manner of a woodlouse. The prolegs then lose their function and contract into the skin. The pupal integument then begins to form inside the larva, and the latter becomes pupiform in shape. The prothoracic shield no longer faces forwards, but upwards, although it still conceals the head. The verrucal setae all lie forwards instead of projecting at various angles.

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* Soluble in 10 per cent. KOH. No action with HCL. Soluble in saturated zinc chloride. Stained by picric acid, and gives off a nitrogenous smell on heating.

In the final phase all the setae lie against the skin, and the intersegmental creases become obliterated, the whole body having a somewhat bloated appearance.

The skin splits first of all in the meson of the prothorax between the divided pigment. After this nothing further happens for some two hours. Then the split is carried back to the region of the metathorax and the head of the pupa is worked out through the breach. The larval skin is then worked backwards over the pupa by means of dorso-ventral flexing of the abdomen. It seems very probable that the backwardly directing spinules on the dorsum of the pupa aid in working off the larval skin—although the spines do not appear to penetrate the skin in the process. Extrication from the larval skin is completed in about twenty minutes.

PUPA

1. Description and Morphology.—The pupae are somewhat flattened dorso-ventrally and have a thin integument through which the development of the imago can be readily observed. Like other Zygaenid pupae they are capable of a considerable amount of movement, belonging to that division of Lepidopterous pupae known as "Incompletae," in which the appendages are not firmly welded to the integument of the body and yet are not completely free. The movable segments of the abdomen are two to six in the female and two to seven in the male.

The average length is 7 mm., average width 3 mm., although there is a slight sexual difference in this respect to which we shall have occasion to refer later.

When newly formed, a pupa is pale yellow with a purple tinge on the dorsum of the abdomen due to the evanescent pigment of the larval dorsum which persists for a time after the final moult. As development proceeds, the colour becomes much darker in the anterior part of the body, until in the final stage before emergence of the adult the characteristic colours of the moth showing through the transparent pupal integument make the whole pupa appear almost black. We give a full description below of the various phases in the development of the pupa.

The junction of the thorax and abdomen dorsally is at about two-fifths the length from the anterior end and is conspicuous in those pupae the thorax of which has become darkened (see Fig. 41).

The pupa is glabrous with the exception of two pairs of minute hairs on the fronto-clypeus (Fig. 42).

The Head.—Pilifers distinct. Labial palpi can be distinguished in specimens cleared in potash, but they are normally hidden by the maxillae. A pair of short, blunt appendages seem to articulate laterally with the base of the maxillae. These are possibly maxillary palps.*

There is no suture between the frons and the clypeus. The antennae

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* Tillyard, 1926, says that maxillary palpi are not found in pupae of the "Incomplete" type.

show distinct segmental divisions; and the bipectinated condition of the adult organ is forecasted by a longitudinal groove in the pupal sheath extending up the proximal eight-ninths of the organ.

There is no marked sexual difference in the antennae of the pupa.

The posterior extension of the antennae and maxillae varies. Together with the metathoracic legs, they may reach almost to the posterior segment of the abdomen, and there is no constancy as to which of the three above-mentioned appendages has the farthest posterior extension (Fig. 43).

The Thorax.—Pronotum narrow; mesonotum about five times as wide. The mesoscutellum overlaps about half the metanotum. The thoracic spiracles open laterally into an enclosed cavity formed by the antenna sheath apposed to the angle between the pro- and meso-thorax. This cavity is closed ventrally by the front femur; while dorsally it has a triangular lumen.

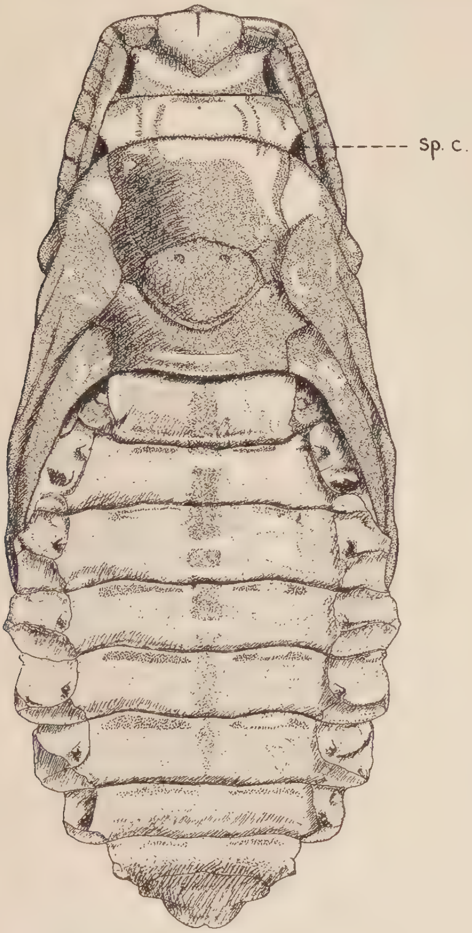

FIG. 41.—*Levuana iridescens.*—♀ pupa—dorsal view, × 25. This pupa was just starting to become pigmented on the thorax, *i.e.* about three days from maturity. *sp.c.*, cavity into which opens the prothoracic spiracle.

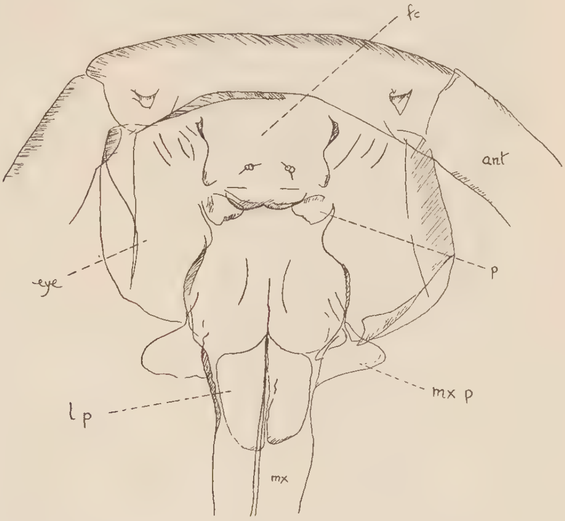

FIG. 42.—*Levuana iridescens.*—Head and appendages of pupa. Drawn from a ♂ pupal skin. Ventral view, × 80. *ant.*, antenna; *fc.*, fronto-clypeus; *p.*, pilifer; *mx.p.*, ? maxillary palp; *l.p.*, labial palp; *mx.*, maxilla.

There is nothing remarkable in the structure or position of the wings and legs.*

Abdomen.—The segments are clearly defined by the somewhat depressed intersegments, with the exception of the posterior two segments.

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* The figure of the pupa by Knowles was probably drawn from a spirit specimen in which the wings had become detached distally from the normal position against the body.

The surface of the abdomen presents an uneven appearance owing to a slight creasing and folding of the integument, particularly about the dorsal aspect of the pleura.

Only seven segments are visible ventrally, the anterior three being hidden by the wing sheaths. The fat body and dorsal vessel can be seen clearly through the integument.

On the dorsal aspect of the pleura of segments 3 to 6 inclusive is a transverse fold which limits posteriorly the somewhat raised anterior part, and anteriorly the more depressed posterior part of each pleuron. On segments 1 and 2 there is a similar pleural fold, but the portion of the pleuron lying anterior to the fold is not raised, being closely overlaid by the hindwing sheath. In the seventh segment the transverse pleural fold is not developed, but the whole pleuron is concave dorsally and clearly separated from the tergum by a longitudinal fold. In the eighth segment the surface of the pleuron is less uneven and there are no distinct folds.

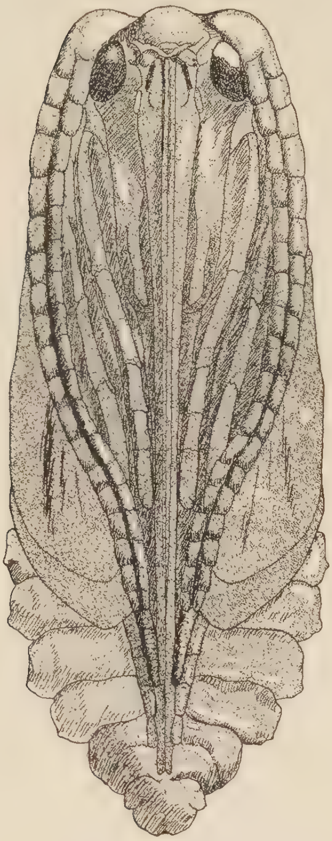

FIG. 43.—*Levuana iridescens.*—♂ pupa—ventral view, × 25. This pupa was drawn a day before the moth emerged.

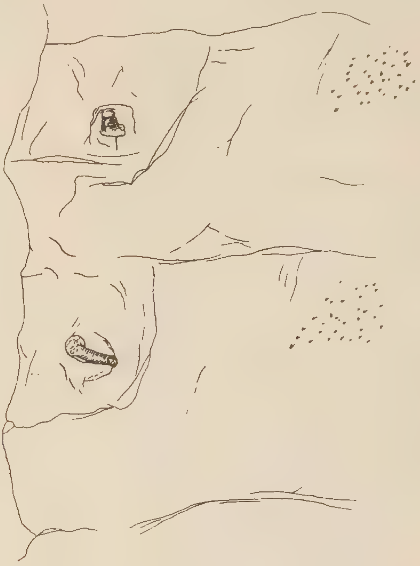

FIG. 44.—*Levuana iridescens.*—Pupa—dorsal view of fifth and sixth abdominal pleura of left side, showing position of spiracles on the raised anterior part. A portion of the respective tergites with chitinous spines is also shown. Drawn from the cast skin of a ♂ pupa, × 84.

These folds of the pleural integument have relation to the spiracles and are not formed on the last two abdominal segments, which are devoid of spiracles.

The spiracles on segments 1 to 6 inclusive each opens at the tip of a small conical projection of the integument (Fig. 44). In segments 1 and 2 these spiracular processes point somewhat laterally and are situated in the depressed area beneath the wing sheath. In segments 3 to 6 inclusive, the processes point upwards and are on the raised anterior part of each pleuron. The seventh spiracles open on smaller prominences with a more lateral aspect on the outer side of the pleural fold. The eighth spiracles are rudimentary and not served by a trachea. They open on the lateral edge of the pleura on a small convexity.

The eversible glands of the second and seventh segments in the larva persist in the pupa, although they are probably functionless, since the pore is permanently closed and the walls do not display any movement. That of the second segment is just visible in a dorsal view although partly hidden by a wing sheath. The position of the seventh segment gland can only be made out in a lateral view ; the gland is not clearly defined.

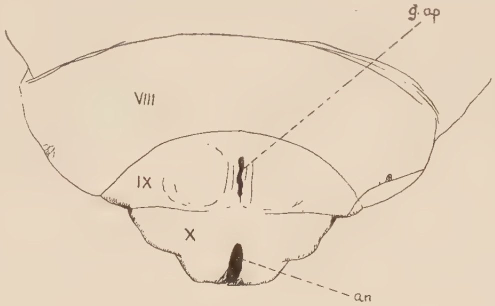

Fig. 45.—*Levuana iridescens.*—♂ pupa, × 84 (cleared in KOH). Terminal segments to show : *an.*, anus ; *g.ap.*, genital aperture. Segments numbered VIII, IX, X.

The anus (Fig. 45) is a slit-like opening at the posterior extremity of the body. On account of its heavily chitinised walls it is fairly conspicuous.

The cremaster is greatly reduced ; all that remains is a transverse line of some three to six small chitinous tubercles on the dorsal part of the anal (tenth) segment. These tubercles are obviously homologous with the cremaster of the higher Lepidoptera. In *Levuana* the organ can have no anchoring function (Fig. 47). The usual number of tubercles is four or five ; but we have found pupae with only three and others with as many as six, the number being quite irrespective of sex. It seems probable that these processes are used to protect the pupa from a backwards movement when extricating itself from the cocoon.

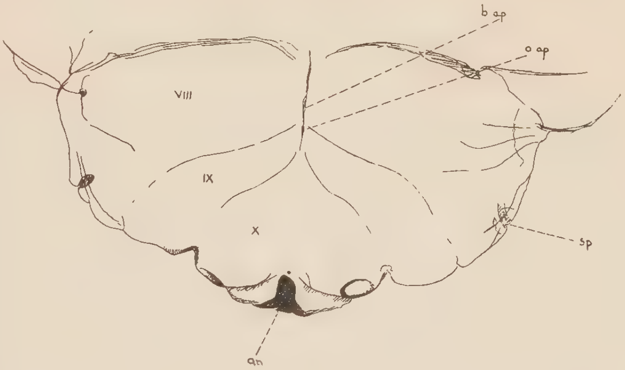

Fig. 46.—*Levuana iridescens.*—Pupa (cleared in potash). Terminal segments of ♀, ventral view, × 84, to show : *b.ap.*, aperture of bursa copulatrix ; *o.ap.*, aperture of oviduct ; *an.*, anus ; *sp.*, functionless spiracle of eighth segment.

On the terga of abdominal segments 2 to 8 inclusive, on either side of the median line is a transverse band of minute backwardly directed chitinous spines (see Figs. 44 and 48). The position of these bands is shown in Fig. 44 in the anterior part of each tergite. It seems likely that these spines assist the pupa in emergence from the old larval skin ; since, being glabrous dorsally, there are no hairs with which to get a purchase on the old skin. The sexes can be distinguished in this stage by the size and shape of the pupa, together with the structure of the genital apertures (Figs. 45 and 46).

In the following table are given (in millimetres) the length and maximum width of thirty-two female and twenty male pupae. The female pupa is slightly larger than the male. The maximum width of the female is usually at the fourth abdominal segment, whereas in the male all the central part of the body is of even width.

Table showing Pupal Measurements in Millimetres.

	Length.			Width.		
	Max.	Min.	Mean.	Max.	Min.	Mean.
Male . . .	7·4	6·3	6·8	3·1	2·6	2·7
Female . . .	7·9	6·5	7·3	3·5	2·7	3·1

The appearance and position of the genital apertures affords a ready distinction between the sexes. In the male there is a single genital aperture situated midventrally on the ninth abdominal segment. It appears as a dark, median, longitudinal slit with two parallel " creases " on each side. In specimens treated with KOH, a subcircular, rather ill-defined plate can be distinguished on either side of the pore. This is simply a part of the sternum marked off by a crease.

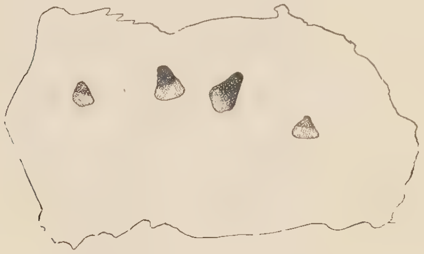

Fig. 47.—*Levuana iridescens.*—Cremaster of pupa—with part of torn-away dorsum of anal segment. × 330.

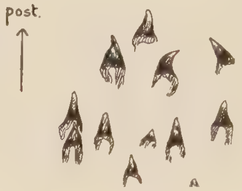

Fig. 48. — *Levuana iridescens.* — Pupa. Chitinous spines on second abdominal tergum. × 700.

In the female the paired nature of the genital opening can be made out under the microscope in cleared specimens ; but the whole structure is much less conspicuous than that of the male ; and, when not obscured by the distal part of the overlying thoracic or cephalic appendages, can with the aid of a lens be distinguished merely as a longitudinal crease. The shape of the sterna of the posterior three segments is also different from the male.

Another sexual difference of less significance is the slightly larger eyes of the male. Thus the ratio between the width of the head (exclusive of antennae) measured ventrally and the total length of the pupa is about 1 : 5 in the male and 1 : 6 in the female.

2. Colour Changes undergone by the Pupa during Development.—Owing to the fact that the pupal integument is thin and unpigmented, the appearance of the pupa changes considerably during maturation owing to the developing colours of the enclosed imago.

We append the following summary of the changes undergone and the periods concerned :—

First day after pupation.—General colour still pale yellow ; but some of the pigment on the abdominal terga is paler, and on the pro- and mesothorax nearly lost altogether. Eyes beginning to pigment internally.

Second day.—Dorsal pigment lost completely—body a rather clouded yellow. Eyes beginning to pigment slightly on the ventral surface.

Third day.—Eyes reddish-brown ventrally, still unpigmented on the dorsal surface. General body colour the same as before.

Fourth day.—Superficial pigmentation of the eyes complete on the ventral surface ; otherwise no change.

Fifth day.—Eyes quite black ; otherwise no change.

Sixth day.—No change.

Seventh day.—Darkening of the thorax just beginning—most pronounced on the metanotum. Appendages still unpigmented.

Eighth day after pupating.—Abdomen still yellow except for a slight darkening of the anal segment. The dark blue colour of the imago now fully formed in the head and thorax and their appendages.

Ninth day.—Abdomen much darker ; scaling of imago visible through the pupal skin.

Tenth day.—Emergence of adult.

3. Occurrence and Habits.—The pupal period is spent within the small white cocoon. Owing to the rather limited space afforded by that part of the coconut tree usually selected for pupation, the cocoons are often massed together in large numbers, but it seems likely that this massing may also be due in some degree to a gregarious instinct assumed at the time of pupation, because when kept in captivity cocoons are often formed on top of one another when there is ample space available for each to be constructed separately. This habit of massing together cocoons is responsible for much of the brood mortality which takes place in a large outbreak.

After the final larval ecdysis has taken place, the pupa lies freely within the cocoon with the ventral surface against the basal platform. It is quite unattached to the cocoon at any point.

Emergence invariably takes place in the morning—generally during the first two or three hours of daylight, the pupa pushing its way through the anterior end of the cocoon. This is done by flexing the abdomen and arching up the centre of the body and then flattening itself again. In this way it prizes up the loosely attached lid of the cocoon and, provided there is nothing to prevent its free egress, it will emerge at least halfway from the cocoon before the skin ruptures and the adult moth crawls out, leaving the pupal skin projecting from the cocoon (see Plate XXVIII, D). These old pupal skins very soon become brushed or blown away in the field except when lodged in a very sheltered position, so that their absence from the end of a cocoon is not a certain indication that the adult has not yet emerged.

When, as often happens in the field, a cocoon is overlaid by others, the pupa from the first-formed cocoon meets the side of another pupa or cocoon in its passage out; being only able to progress in one direction, it will eventually die, generally before the adult has started to emerge. Pupae which have died in this manner are a very characteristic feature of any sample of massed cocoons. In their efforts to force their way through the neighbouring obstruction they become much flattened out and the wings and legs are often pushed out so as to lie at the side of the body (see Plate XXVIII, B). It is thus quite easy to attribute the cause of death to such pupal relics, even though they may become mutilated to some extent subsequently by scavenging insects and mites.

We have already remarked that the pupae are capable of a considerable amount of movement. This power is most in evidence during the process of emergence from the cocoon. But it is also made use of when the pupa emerges from the last larval skin. During the first few days after pupation a pupa has often been observed to bend the abdomen slowly from side to side. This movement is continued with decreasing frequency until the pupa is mature. The reason for this movement is not known, unless it be a sort of precaution against upsetting within the cocoon, for if the ventral surface of the pupa came to lie against the lid of the cocoon the pupa would experience much difficulty in emerging.

THE ADULT

1. Size.—The females, on the average, are larger than the males. The wing expanse is as follows:—

(*a*) *Females.*	Average for 20 specimens . .	16·3 mm.
	Maximum	17·5 mm.
	Minimum	15·0 mm.
(*b*) *Males.*	Average for 20 specimens . .	14·1 mm.
	Maximum	15·0 mm.
	Minimum	13·1 mm.

2. Colour.—The descriptions given by Bethune-Baker and Jordan (see "Systematic") of the colouring of the adult *Levuana iridescens* are not accurate. They were made from dried specimens, and the colour always fades and changes considerably when the adults are set and dried. The following description applies to living or freshly-killed specimens:—

(*a*) General Appearance.—Upper surface, dark metallic purple, except abdomen, which is ochreous. Hindwings semi-transparent.

(*b*) Details.—*Head.*—Dorsal surface of head, upper half of frons, and antennae dark green-blue with brilliant metallic sheen. Lower half of frons, palpi, and a narrow band bordering eye ventrally, ochreous and without sheen. Eyes black.

Thorax.—Prothorax and tegulae the same as the dorsal surface of head,

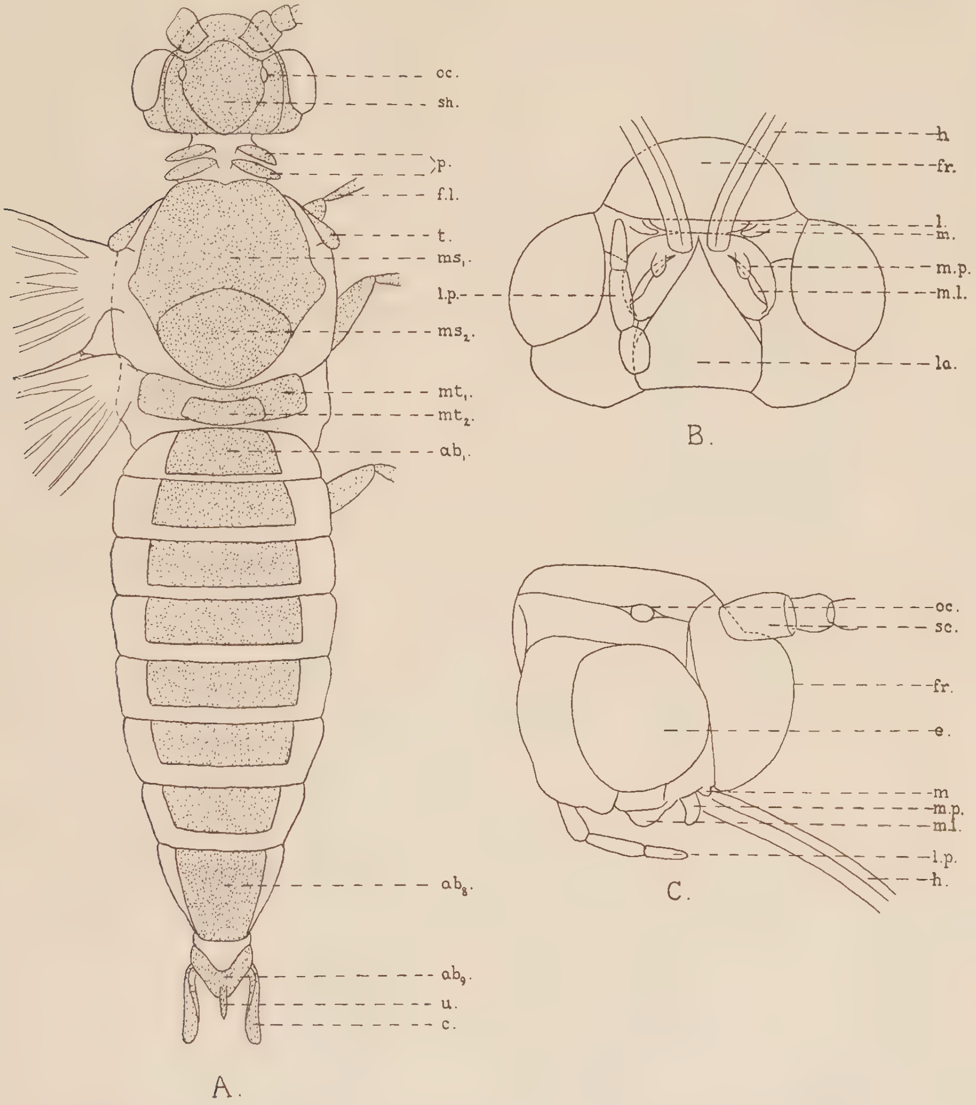

FIG. 49.—*Levuana iridescens.*—A. Diagrammatic dorsal view of male (scales removed), × 33. B. Ventral view of head (diagrammatic), × 75. C. Right lateral view of head (diagrammatic), × 75.

ab.$_1$, first abdominal tergite; *ab*.$_8$, eighth abdominal tergite; *ab*.$_9$, ninth abdominal tergite; *c*, clasper; *e*, eye; *fl*, foreleg; *fr*, frons; *h*, haustellum; *l*, labrum; *la*, labium; *lp*, labial palp; *m*, mandibular vestige; *m.l.*, maxillary lobe; *m.p.*, maxillary palp; *ms*$_1$, mesoscutum; *ms*$_2$, mesoscutellum; *mt*$_1$, metascutum; *mt*$_2$, metascutellum; *oc*, ocellus; *sc*, scape; *sh*, head "shield"; *t*, tegula; *u*, uncus.

etc. Remainder of dorsal surface of thorax, and whole of ventral surface, similar, but with purple tinge. Whole of thorax highly metallic.

Wings.—Upper side of forewings uniformly dark metallic purple except basally, where purple merges into colour of tegulae ; no markings ; scaling of normal density ; fringe same colour as rest of wing. Under side very thinly scaled except at tip and along costal margin, where colour is same as upper side.

Hindwing very thinly scaled on both sides and therefore semi-transparent ; scaling dark but insufficient to produce colour except near margins where wing is purple ; fringe purple.

Legs.—Foreleg : coxa, trochanter, and femur blueish-ochreous, tibia and tarsus ochreous. Middle and hind legs : coxae same as ventral surface of thorax, femora green-blue basally, shading to blueish-ochreous distally, tibiae and tarsi ochreous.

Abdomen.—Dorsal surface : first and last segments same colour as meso- and meta-thorax ; remaining segments ochreous with blue tinge near middle line. Ventral surface : ochreous throughout with very faint blue tinge mid-ventrally, particularly on the more anterior segments.

(*c*) VARIATION.—There is very little variation in colour. The intensity of the purple tinge on the thorax and wings and the amount of blue on the legs and abdomen vary slightly in each sex. Otherwise the colouring is constant.

(*d*) SEXUAL DIMORPHISM IN COLOUR.—There is less blue tinge on the abdomen (dorsally and ventrally) and on the legs of the male than the female. Sometimes there is no blue at all on the under side of the male. Otherwise the colour is exactly the same in both sexes.

3. Morphology.—FEMALE.—*Head* (Fig. 49).—The frons is prominent and strongly convex, projecting considerably in front of the eyes. When viewed dorsally it is nearly semicircular in outline. The central part of the epicranium, which is clearly outlined by sutures, is shield-shaped. Its length is a little greater than its width, and the ocelli, which are conspicuous, are situated just behind the anterior angles of the " shield." That part of the epicranium which lies, on either side, between the " shield " and the eye, and behind the frons, bears many short erect hairs. The ventral surface of the head is occupied chiefly by the mouth parts. The whole of the head, except the eyes and the mouth-parts, is heavily scaled. The eyes are smooth and hairless.

Antennae.—The antennae in this sex (Figs. 50, 51, and 52) are bipectinated in such a way as to appear to the naked eye somewhat clubbed ; that is to say, the pectinations on the more basal segments are very short, consisting of little more than a pair of longitudinal prominences on each of these segments, while those of the more distal segments of the funicle are long. There is a gradual increase in length of the pectinations from the base of the funicle towards the extremity, until at about two-thirds of the length of the funicle from the base the pectinations reach their maximum length. Beyond this point they decrease in length but are still long.

The scape is large and swollen. The pedicel is short, its length being about one-third of that of the scape. The basal segments of the funicle are only slightly longer than the pedicel, but the segments of the funicle increase in length distally until in the distal third of the latter they are as long as the

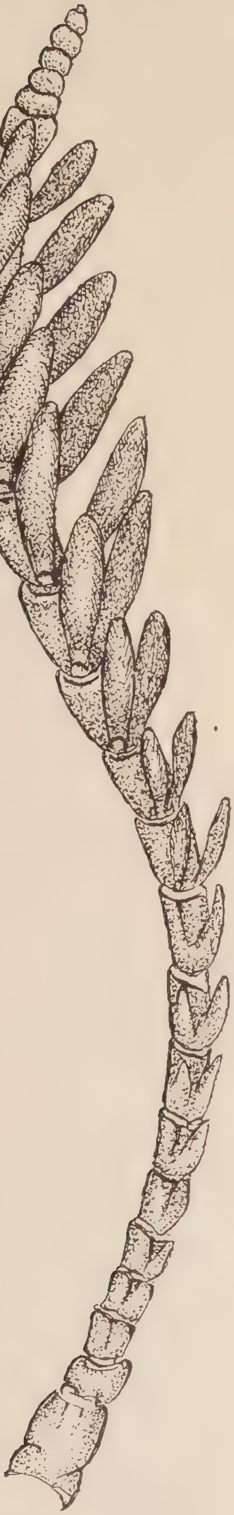

FIG. 50.—*Levuana iridescens.*—Antenna of female. × 40.

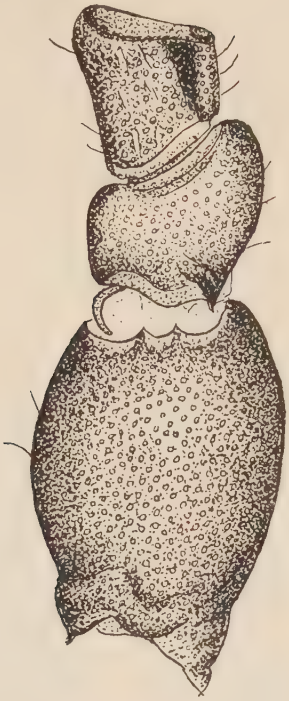

FIG. 51.—*Levuana iridescens.*—Scape, pedicel, and first segment of funicle of female antenna. × 130.

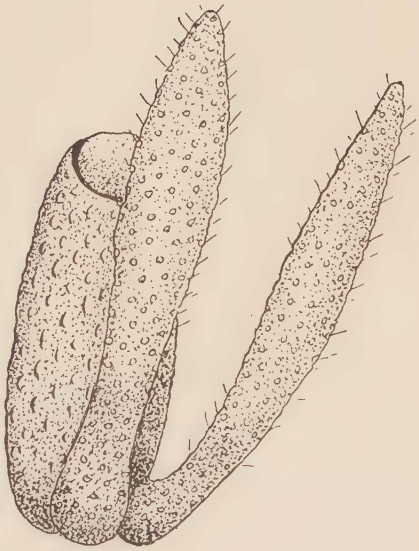

FIG. 52.—*Levuana iridescens.*—Eleventh segment of funicle of female antenna. × 130.

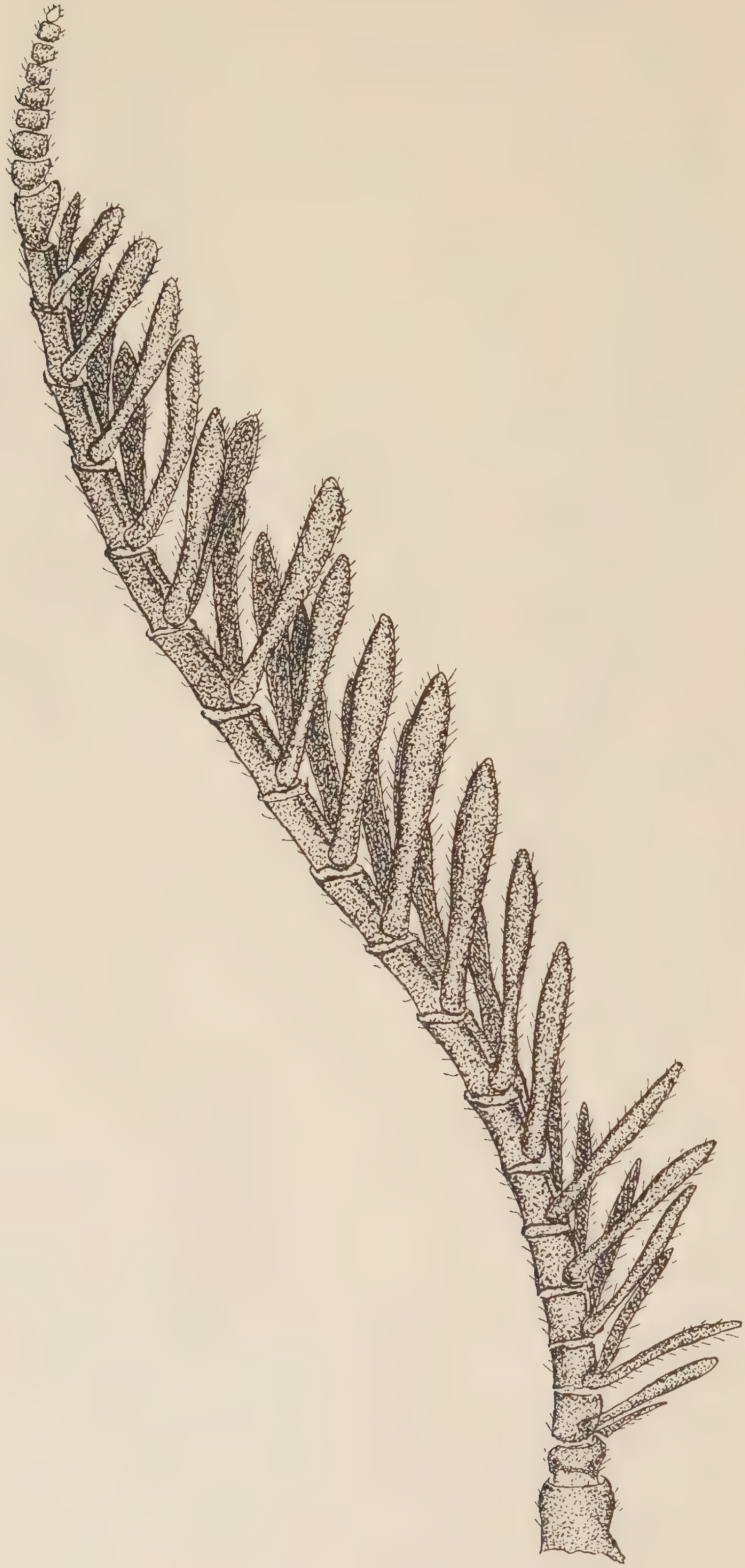

FIG. 53.—*Levuana iridescens*.—Antenna of male. × 40.

scape. There are seventeen segments in the funicle as a rule, but almost as often there are eighteen. Intermediate forms between these two conditions frequently occur, the basal segment of the funicle in these forms being very long and apparently formed by the fusion of two segments. The funicle is grooved along its inner surface. The pectinations are elongated and somewhat spatula-shaped ; they bear many short hairs.

The antenna terminates in a short club, which consists of not more than nine annular segments. The exact number of segments varies from seven to nine, there being a marked tendency for two or three of the penultimate segments to fuse together. The basal segment of the club is considerably larger than the remainder, and the segments diminish in size successively towards the extremity of the antennae. The club is entirely without pectinations and is not grooved. The antennae are densely scaled.

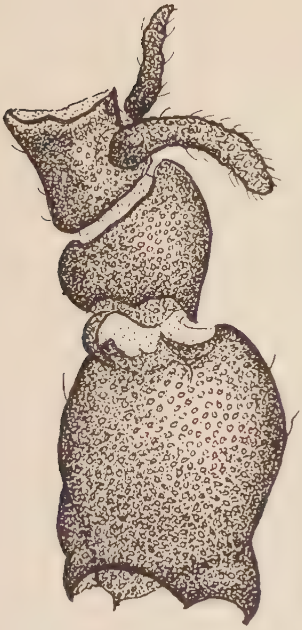

Fig. 54.—*Levuana iridescens.*—Scape, pedicel, and first segment of funicle of male antenna. × 130.

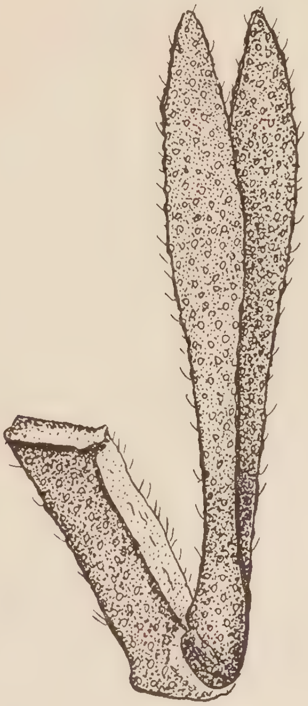

Fig. 55.—*Levuana iridescens.*—Eleventh segment of funicle of male antenna. × 130.

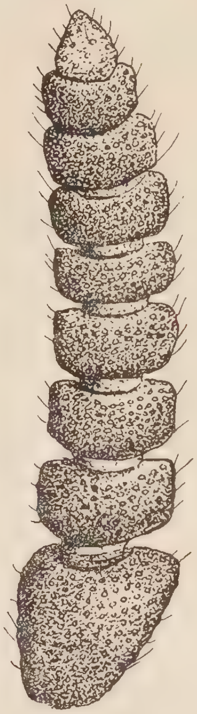

Fig. 56.—*Levuana iridescens.*—Antennal club of male. × 130.

Mouth Parts (cf. Fig. 57).—The mouth parts are well developed and are functional.

The labrum is a narrow transverse plate attached to the ventral edge of the fronto-clypeus and directed backwards. Its central region is almost transparent, being very little chitinised, but its two ends are strongly chitinised and slightly swollen. The swollen portion on either side is homologous with the pilifers of other species, but since the labrum is almost flat and its posterior border is almost straight, the pilifers are not clearly differentiated. Each pilifer bears about twenty long, stout spines directed inwards and backwards. The remainder of the labrum bears a few, sparsely-scattered, minute hairs.

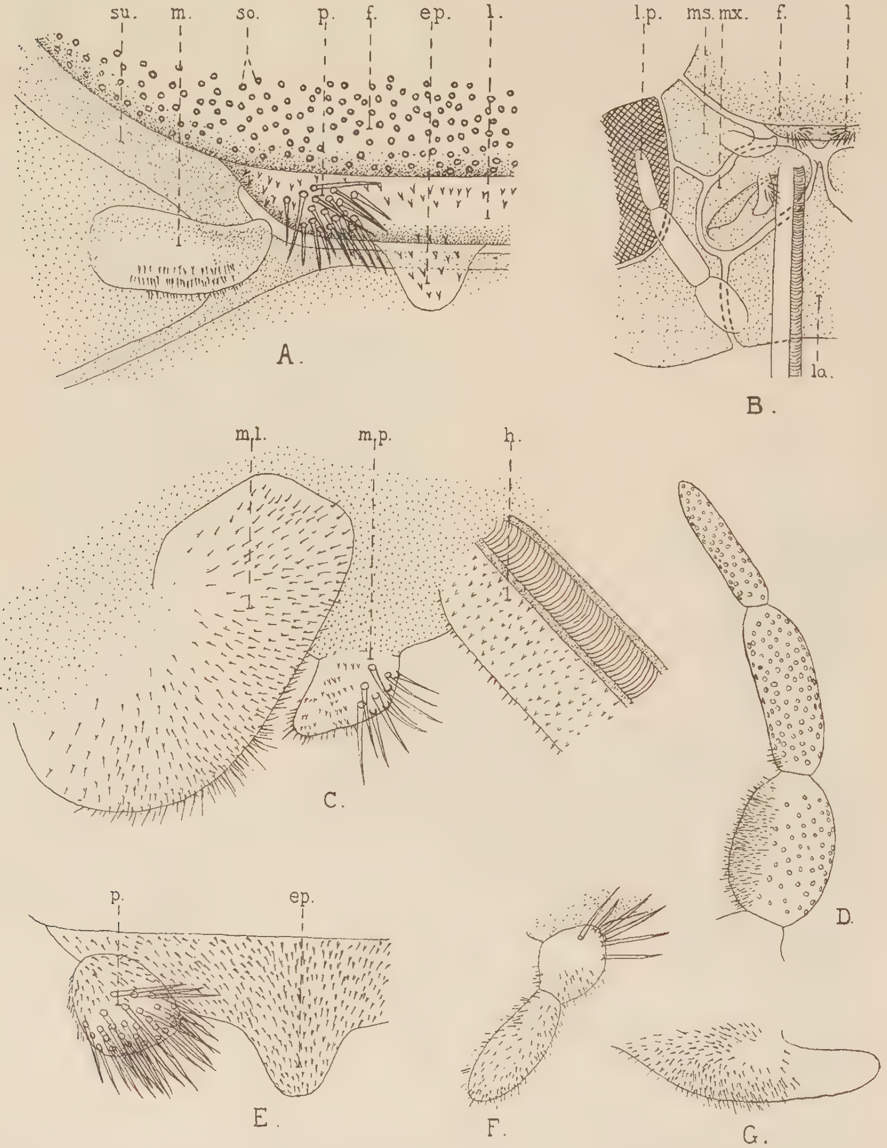

FIG. 57.—*Levuana iridescens.*—Mouth parts (ventral view). A. Labrum and mandibular vestige (right side only), × 200. B. Ventral view of head (right side only), with sclerites separated to show relation of mouth parts (diagrammatic). C. Maxillary appendices of right side, × 400 (the maxillary lobe is folded over towards the palp). D. Left labial palp, × 20. *Artona trisignata.*—E. Labrum (right side only), × 180. *Artona albicilia.*—F. Right maxillary palp, × 350. G. Right mandibular vestige, × 200. *e.p.*, epipharynx; *f.*, fronto-clypeus; *h.*, haustellum; *l.*, labrum; *la.*, labium; *l.p.*, labial palp; *m.*, mandibular vestige; *m.l.*, maxillary lobe; *m.p.*, maxillary palp; *m.s.*, mandibular sclerite; *mx.*, maxillary sclerite; *p.*, pilifer; *so.*, scale sockets; *su.*, suture.

The epipharynx is a tongue-like membranous lobe arising from the central portion of the labrum and projecting postero-dorsally into the buccal cavity, but is so delicate as to be most difficult to detect. It bears a few minute hairs similar to those on the labrum. There are no scales on the labrum.

The mandibular sclerites or genae are situated, one on either side, between the labrum and the eyes. From the inner corner of each there arises an elongated, membranous, extremely flimsy sac, which tapers slightly in its distal half. Its extremity is rounded and slightly curved forwards, and its length is approximately half that of the labrum. On its posterior surface there are three or four irregular rows of minute hairs, presumably sensory, but the remainder of its surface is absolutely smooth and transparent. This interesting organ, which is directed inwards and terminates very near the pilifer, occupies the same position as those which are considered to be vestigial mandibles in certain other Lepidoptera and is very probably homologous with the true mandibles of other insects.

The paired maxillary sclerites give rise to the haustellum, the maxillary palpi, and the maxillary lobes. The haustellum is well-developed and is of the usual Lepidopterous form. Its two halves are readily separable and arise near the inner ends of the maxillary sclerites. The maxillary palp is a minute structure situated on the outer side of the basal membrane of the haustellum. It consists of a single stumpy joint without any definite articulation. Its base is broad, and it tapers rapidly to a narrowly rounded apex which is directed backwards and outwards. On its inner surface, near the base, there is a group of about ten stiff bristles, and the remainder of its surface bears very minute hairs arranged more or less in short straight lines which are scattered sparsely over it. When the head is viewed laterally, the maxillary palp can be seen with the naked eye as a minute projection just behind the base of the haustellum. There is never any indication of its being divided into two segments. The maxillary lobe is a prominent strongly chitinised structure which projects ventrally from the maxillary sclerite. In shape it resembles a human ear. Its line of attachment to the sclerite extends obliquely backwards from near the base of the maxillary palp to the postero-lateral end of the sclerite.

Both surfaces of the lobe are covered with minute hairs. The maxillae, including the basal sclerites and their appendages, are entirely devoid of scales, but the basal sclerites are sparsely covered with minute hairs which are arranged roughly in short, straight rows.

The labium is a large sclerite which forms the greater part of the wall of the pit into which the haustellum folds. It is approximately triangular in shape, the apex being directed forwards between the maxillae and the base forming the central part of the posterior edge of the ventral surface of the head. It is concave when viewed ventrally. The labial palpi arise from the basal angles of the labial sclerite, and extend forwards to the level of the labium. Each of the labial palpi consists of three well-developed segments of which the middle segment is rather longer than either of the others and the proximal segment is the broadest and is rounded. The proximal segmen is densely covered with minute hairs on its inner aspect, and the middle segment bears a small group of similar hairs at its base, also on the inner side. The distal segment is devoid of hairs. The labial palpi are densely scaled except in those areas which bear hairs. The labial sclerite is without scales but is clothed, like the maxillary sclerites, with minute hairs arranged more or less in short, straight rows.

The mouth-parts of *Levuana iridescens* are of special interest when compared with those of allied species of the genus *Artona*. They show considerable specialisation in several respects, notably as regards the reduction of the pilifers and of the maxillary palpi. In those species of *Artona* that have been available for examination (*A. trisignata, A. albicilia*, and *A. catoxantha*), the pilifers are present as two very prominent lobes projecting from the ends of the labrum, and the maxillary palpi are two-jointed. Mandibular vestiges, similar to those of *Levuana*, are present in both *A. trisignata* and *A. albicilia*, but they differ from those of *Levuana* in being densely covered basally with minute hairs.

Thorax.—The patagia are present in the form of two pairs of curved chitinous plates, one in front of the other, which are closely apposed to the anterior end of the thorax. The tegulae are well developed. The mesoscutum is strongly convex, and its width is greater than its length. Its anterior edge is emarginated medially. The length of the mesoscutum and mesoscutellum together is approximately equal to the width of the former. The metathoracic tergites are short (antero-posteriorly) and roughly rectangular in outline, the posterior edge of the metascutellum, which is itself nearly rectangular, being colinear with that of the metascutum. The characteristic shape of the thoracic tergites is shown in Fig. 49. The ventral exoskeleton of the thorax is of the usual form.

The thorax is heavily scaled except for the anterior half of the metascutum, which is completely devoid of scales and is densely covered with very minute hairs which are directed inwards.

*Wing Venation.**—The wing venation is peculiar and very characteristic, particularly as regards the condition of the median vein M.

(*a*) *Forewing* (Fig. 58).—The vein Sc is well-developed, separate, and unbranched. The main stem R is very wide as far as the point Q, but at that point it is reduced to half its width. R_1, R_2, and R_3 arise from the cell. R_4 and R_5 are fused together basally but diverge widely distally. The stalk R_{4+5} is nearly always a little longer than either R_4 or R_5, and occasionally it is much longer. R_1, R_2, R_3 and R_{4+5} are nearly equidistant from one another as a rule, but sometimes R_2 and R_3 are much nearer together at their points of origin on Rs than to either R_1 or R_{4+5} respectively. In extreme cases R_2 and R_3 arise from almost the same point on Rs, showing a tendency to coalesce. Rs is well developed as far as R_3, but is vestigial beyond R_3. M_1 originates from the stem R_{4+5} at a point a very short distance from P, which is the angle of the cell. R_{4+5} and M_1 are very faint in the immediate neighbourhood of P; otherwise they are well-developed. M_2 and M_3 arise from the cell, and their points of origin are closely approximated. They never fuse, however.

* The Comstock-Needham system of notation is employed.

Both are well developed except at their points of origin. The cross-vein PTV (*i.e.* M_1, M_2), which closes the cell distally, is very faint and scarcely

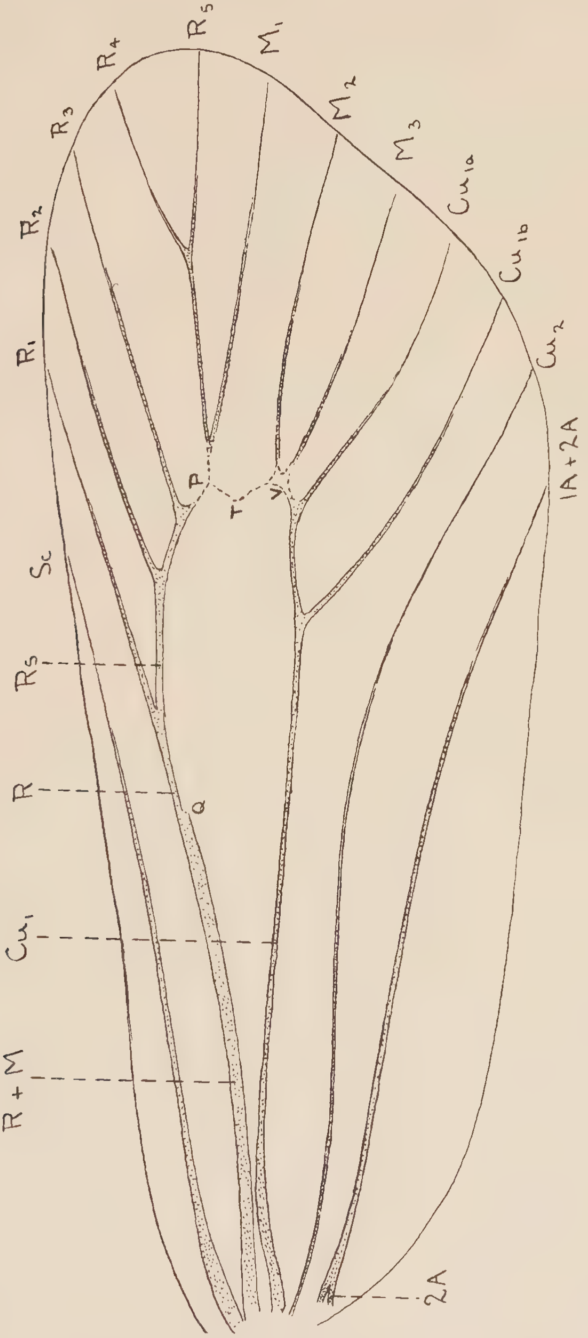
R₅
M₁
R₄
R₃
M₂
M₃
Cu₁a
R₂
Cu₁b
Cu₂
R₁
1A+2A
P
T
V
Sc
Rs
R
Q
Cu₁
R+M
2A

Fig. 58.—*Levuana iridescens.*—Forewing venation (diagrammatic). × 30.

perceptible. It is nearly always bent inwards to a sharp angle at T. T is often much nearer to P than to V and is never farther from P than from V. The angle PTV is sometimes less than 90°, but is usually more, and sometimes the

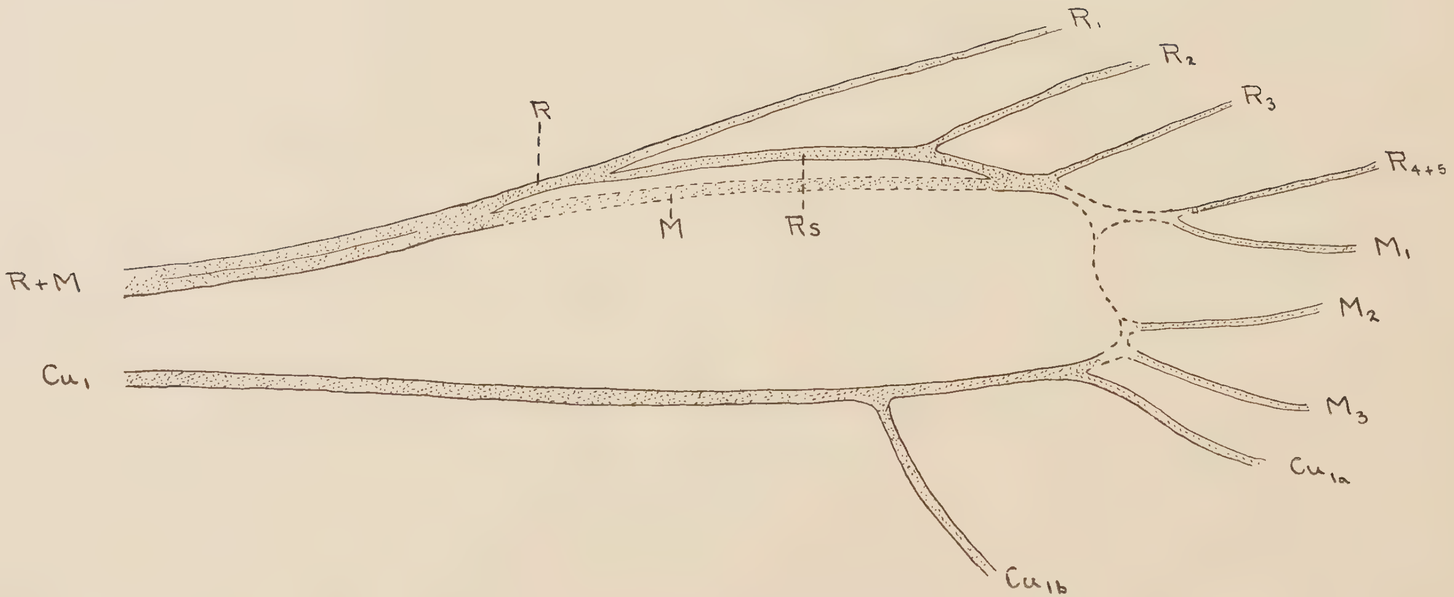
R₁
R₂
R₃
R₄₊₅
R
M
Rs
M₁
M₂
M₃
R+M
Cu₁
Cu₁ₐ
Cu₁b

Fig. 59.—*Levuana iridescens.*—A rare variation of the forewing venation.

cross-vein is almost straight. Cu_1 and Cu_2 and both branches of Cu_1 (*i.e.* Cu_{1a} and Cu_{1b}) are well developed, and Cu_2 is free throughout its length. There is one prominent anal vein which represents 1A and 2A. These two veins are completely fused except for a very short distance at the base of the wing. The fusion is so complete that 2A is only apparent as a very small projection directed inwards from the proximal extremity of anal vein. 3A has completely atrophied. A linear thickening of the wing, which extends for a short distance down the hind margin from the base of the wing, looks at first sight like 3A ; but it is not preceded by a trachea in the pupal wing and therefore cannot be regarded as representing 3A.

In the vicinity of the cross-vein M_1M_2 there is always a vaguely defined area in which the wing membrane is less chitinised and more transparent than elsewhere.

There is never any trace of the main stem M across the centre of the cell in the position in which it would be expected. A fold in the wing usually extends from T towards the base of the wing. This has been regarded as a vestige of M, but a study of the tracheation of the pupal wing shows that this is not the case. The cell is usually absolutely devoid of veins, but very occasionally specimens occur in which there is a faint linear chitinisation of the wing extending across the top of the cell from Q to near P (Fig. 58). It cuts off from the cell a small narrow area which is similar in position to the radial cell or areole of certain other families of Lepidoptera, but it is not homologous with the areole. The pupal tracheation (Fig. 62) shows that this is actually the main median vein (M). The trachea M runs alongside R from the base of the wing to Q, and M and R become incorporated into one thick vein in this region of the adult wing. At Q the trachea M turns slightly away from R and Rs and extends across the cell to T, where it divides into M_1, M_2, and M_3. The portion QT of the trachea M fails to chitinise, and atrophies completely except in those very rare individuals already mentioned, and this explains the sudden narrowing of the vein R (actually R+M) at the point Q in most adults.

An examination of the late pupal wing (Fig. 60) about one day before the emergence of the adult is instructive. By this time the process of atrophy of the tracheae is well advanced and the rudiments of the veins are very apparent. The vein M shows clearly although it atrophies later. It usually extends in a straight line across the centre of the cell from Q to T as in the figure, but sometimes it is very near to Rs throughout its length. When it is near the middle of the cell it atrophies completely before the adult is ready to emerge, but when it is exceptionally near to Rs, so as to come within the region of chitinisation of the latter, it chitinises slightly and so produces the rare variety of the adult wing shown in Fig. 59. It is obvious that when M is very close to Rs throughout its length the points P and T must be very close together. In such cases the cross-vein M_1M_2 consists almost entirely of TV, and is therefore not angulated at all in the centre. It is very noticeable that whenever M is particularly near to Rs the cross-vein is almost straight.

This remarkable condition of M is further discussed in the section dealing with the relationships of *Levuana* (p. 41).

(*b*) *Hindwing* (Fig. 61).—The subcostal vein is well-developed and extends from the base to the apex of the wing nearly parallel to the costal margin. R is completely atrophied basally, but appears as a vestigial vein at a short distance from the base, just behind Sc. It extends outwards parallel to Sc to near the middle point of Sc, where it divides into R_1 and Rs. R_1 turns at its point of origin obliquely towards Sc and fuses completely with it. It is therefore very short and has the appearance of a cross-vein between Sc and R. Rs curves away from Sc + R_1, forming part of the anterior boundary of the cell.

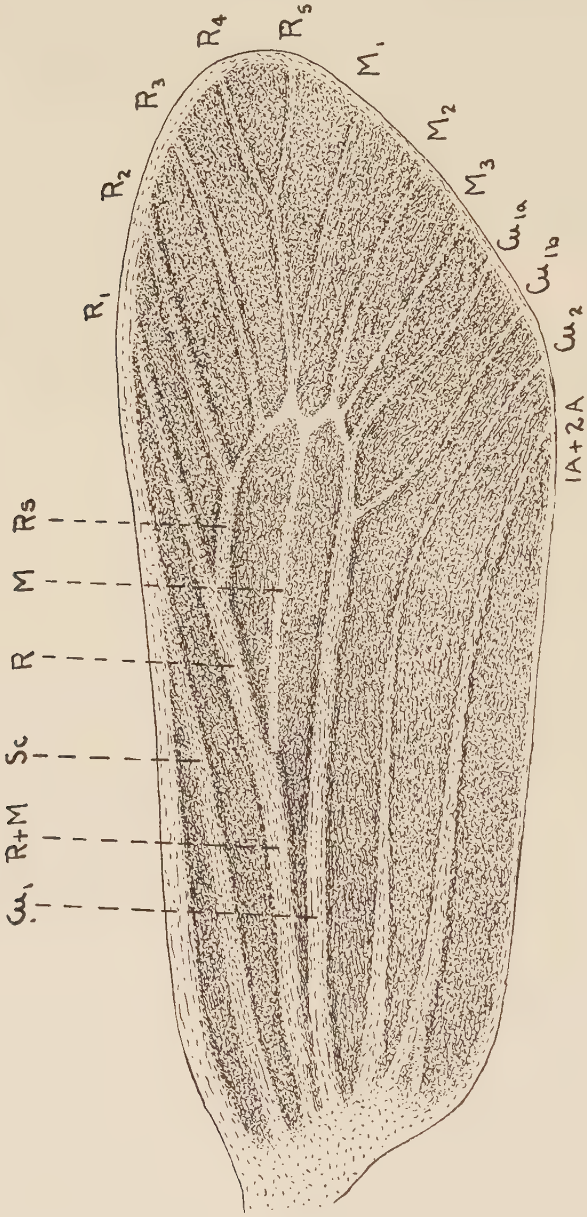

Fig. 60.—*Levuana iridescens*.—Pupal forewing after chitinisation of veins. × 50.

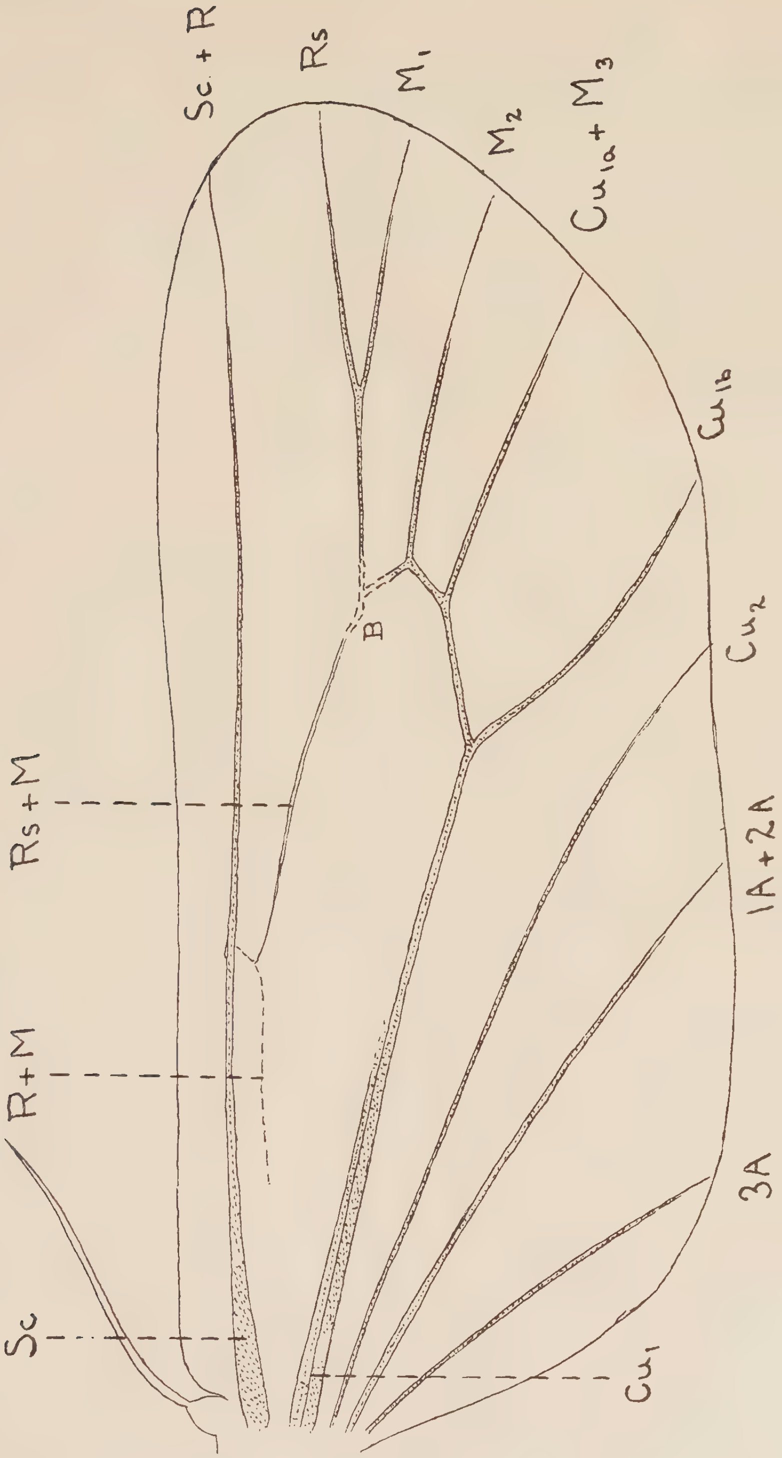
Sc + R
Rs
M1
M2
Cu1a + M3
Cu1b
B
Cu2
Rs + M
R + M
1A + 2A
3A
Sc
Cu1

FIG. 61.—*Levuana iridescens*.—Hindwing venation (diagrammatic). × 33.

It turns towards the apex of the wing sharply at B, and proceeds to the margin without dividing. Rs is usually very thin, especially where it bounds the cell. There is considerable variation in the degree of chitinisation of R, R_1, and the proximal part of Rs, all of which are sometimes so thin and transparent as to be scarcely visible. M_1 is present but is fused proximally with Rs for about half its length. The point of separation of Rs and M_1 varies considerably. Sometimes their common stalk is longer than the free part of either, sometimes shorter. There is only one other median vein, and this is M_2. M_3 and Cu_{1a} have fused together completely. M_2 arises from the cell midway between Rs, M_1, and $Cu_{1a}+M_3$. Cu_{1b} arises from the lower angle of the cell and is widely separated from $Cu_{1a}+M_3$. Cu_2 is complete and well developed. There are two anal veins, of which the first represents 1A and 2A completely fused, while the other is 3A. The cross-veins which close the cell distally are well developed.

Cu_1 is very well developed. In most specimens it has the appearance of two veins in close contact with one another. This appearance suggests that the main stem M, of which there is never any trace within the cell, has fused with Cu_1, but actually this is not the case. The tracheation of the pupal wing (Fig. 63) shows that the absence of M within the cell is due to the fact that it has fused completely with R and Rs, a condition which is similar to that which occurs in the forewing. The cell in the pupal wing is bounded anteriorly by two tracheae which extend side by side nearly parallel to the trachea Sc. These are R and M. The trachea R divides into R_1 and Rs. R_1 turns away from Rs so as to run alongside Sc for the rest of its length. M divides near the end of the cell into M_1, which runs alongside the distal part of Rs and M_2. The venation of the adult is produced by the complete fusion of M with R and Rs, of M_1 with Rs, and of R_1 with Sc. Cu_1, in spite of its double appearance, is formed by the chitinisation of a single trachea.

The phylogenetic significance of the fusion of M and R has already been discussed (p. 49).

(c) *The Missing Vein in the Hindwing.*—The arrangement of the tracheae in the pupal forewing is absolutely constant (Fig. 62). In the pupal hindwing, however, the tracheae vary to a great extent, a circumstance which is of the greatest importance in identifying the veins of the adult hindwing. It is at once obvious that one median vein or else the anterior branch of Cu_1 is missing in the adult hindwing, but no matter how carefully the venation is studied it is impossible to say whether the missing vein is M_1, M_2, or Cu_{1a}. No clue can be obtained by a study of the wings of other Zygaenids, for although in *Artona* M_3 is evidently undergoing coalescence with Cu_{1a}, there is no reason to assume from this that the same thing has happened in *Levuana*, since the two genera are specialised in such different ways in other respects.

The account which has just been given of the hindwing tracheation applies only to typical specimens. This typical arrangement is illustrated in Fig. 63. The deviations from this form are three in number and are associated with the tracheae Rs, M and its branches, and Cu_1 and its branches. All the other tracheae are constant. All three variations are of common occurrence, and sometimes two of them occur in the same specimen, one in the left wing and the other in the right.

The first variation (Fig. 64) is characterised by the presence of an additional branch of the trachea M and by the absence of one branch of Cu_1. That is to say, M is three-branched as in more primitive species and Cu_1 is unbranched. The additional branch of M arises from M_2 (cf. Fig. 63) and is certainly M_3. The missing branch of Cu_1 is Cu_{1a}. The homologies of the tracheae are easily determined by considering the parts of the wing which they supply.

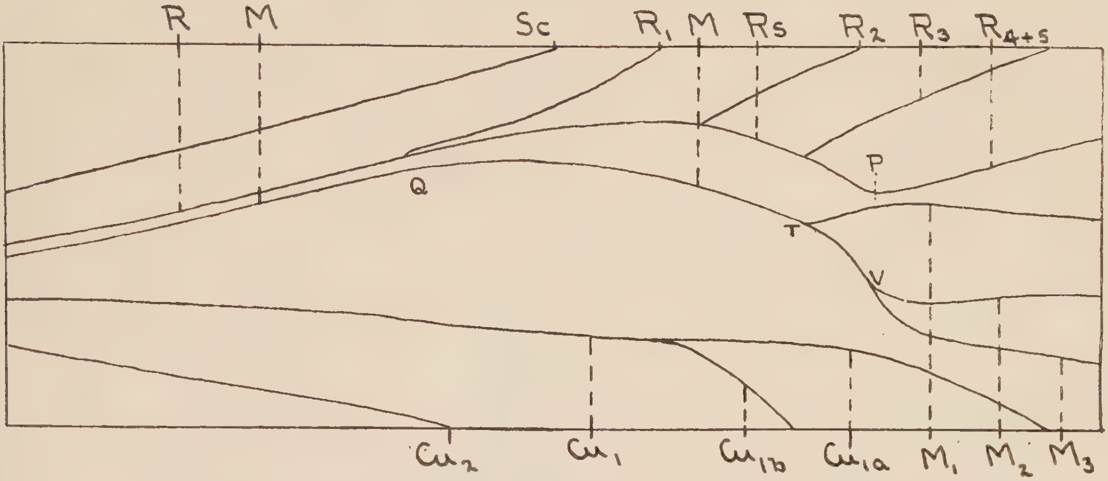

FIG. 62.—*Levuana iridescens.*—Tracheation of central region of pupal forewing (diagrammatic).

The second variation (Fig. 65) is very remarkable in that Rs is two-branched. The additional branch supplies that part of the wing which is normally supplied by M_1, and is therefore called M_1 in the figure, though actually it is not a branch of M. M is two-branched, but the branches are M_2 and M_3 instead of being M_1 and M_2 as in typical specimens. Cu_1 is unbranched, since the trachea Cu_{1a}

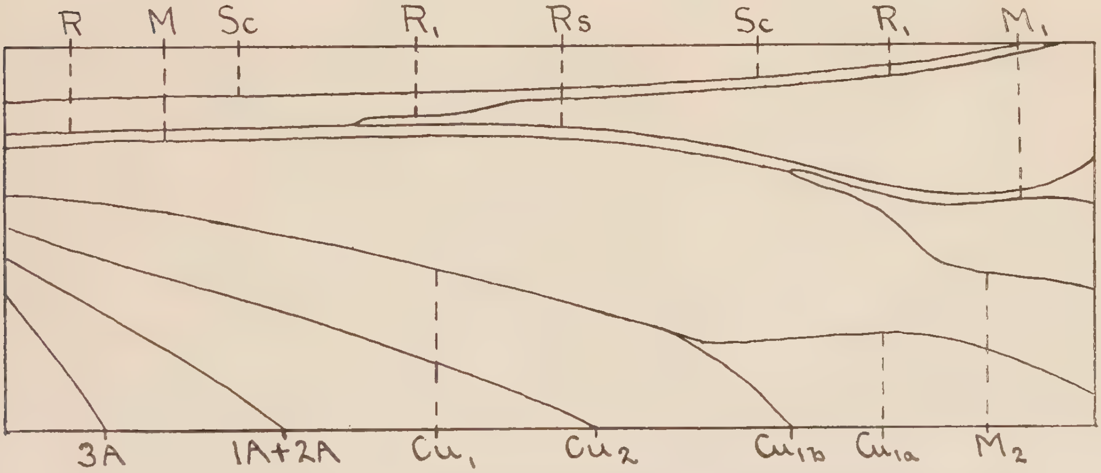

FIG. 63.—*Levuana iridescens.*—Tracheation of central region of pupal hindwing (diagrammatic).

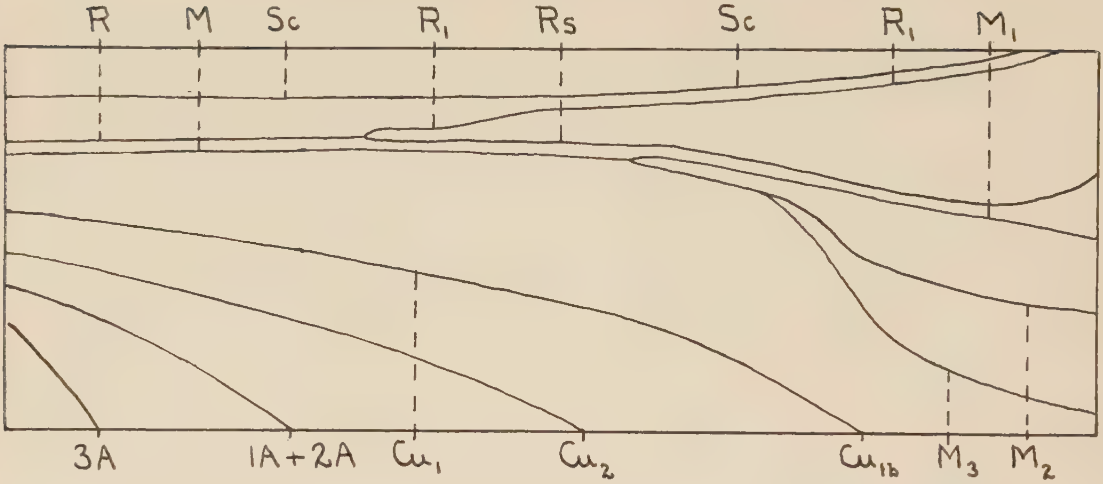
R
M
Sc
R1
Rs
Sc
R1
M1
3A
1A+2A
Cu1
Cu2
Cu1b
M3
M2

FIG. 64.—*Levuana iridescens.*—Variation in tracheation of pupal hindwing (diagrammatic).

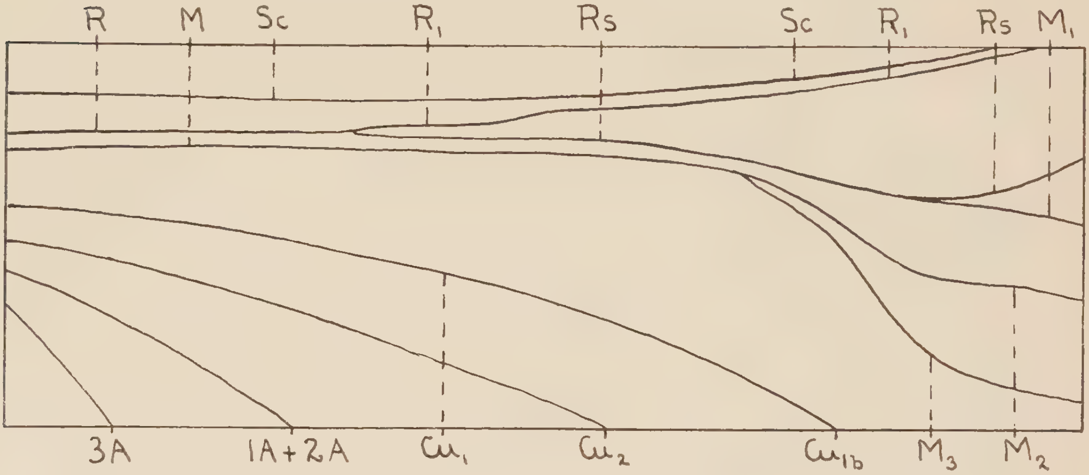
R
M
Sc
R1
Rs
Sc
R1
Rs
M1
3A
1A+2A
Cu1
Cu2
Cu1b
M3
M2

FIG. 65.—*Levuana iridescens.*—Variation in tracheation of pupal hindwing (diagrammatic.)

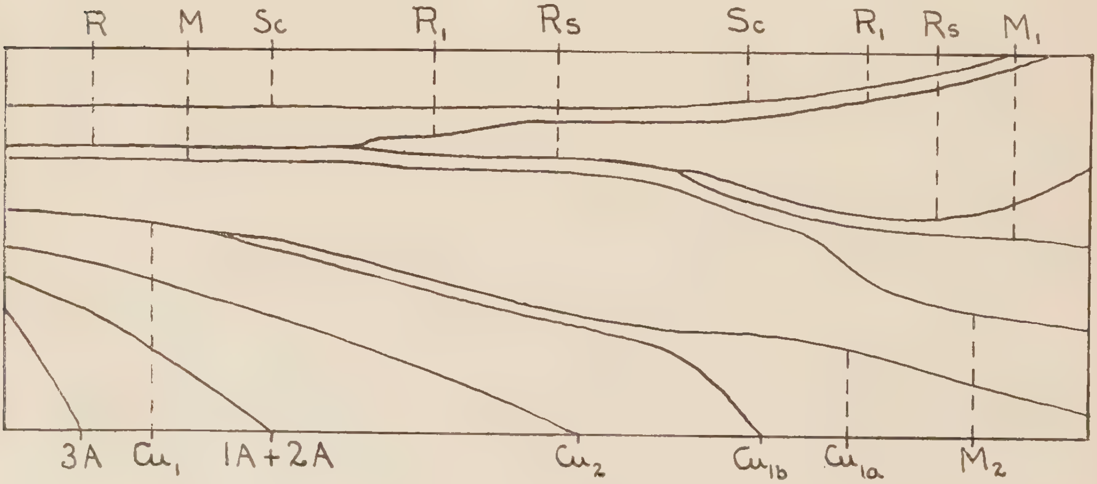
R
M
Sc
R1
Rs
Sc
R1
Rs
M1
3A
Cu1
1A+2A
Cu2
Cu1b
Cu1a
M2

FIG. 66.—*Levuana iridescens.*—Variation in tracheation of pupal hindwing (diagrammatic.)

is missing, and that part of the wing which would normally be supplied by Cu_{1a} is supplied by M_3.

In the third variation (Fig. 66) we again find Rs two-branched, but Cu_1 in this case is also two-branched, while M has no branches at all. M supplies that part of the wing which is normally supplied by M_2.

These variations explain in a striking manner the peculiarities of the adult hindwing. In spite of the diversity in arrangement of the tracheae we find that the total number of tracheae, and their positions in the distal part of the wing, are constant in all specimens. When one extra trachea arises from M or Rs, Cu_1 has one branch less, and when M loses a branch Rs gains one. We have already seen that in the course of time M has become approximated to R and Rs, so that in typical specimens (Fig. 63) the two branches of M arise from a point very close to Rs. It is therefore immaterial, so far as the aeration of the wing is concerned, whether the trachea M_1 actually arises from M or from Rs. The fact that the point of origin of M_1 does actually vary in this manner shows that the approximation of M to Rs has almost amounted to fusion and indicates that *Levuana* will eventually attain a condition in which the tracheae M and R are completely fused, so that Rs, M_1, and M_2 are branches of a single trachea just as the veins Rs, M_1, and M_2 are branches of a single vein in the existing hindwing.

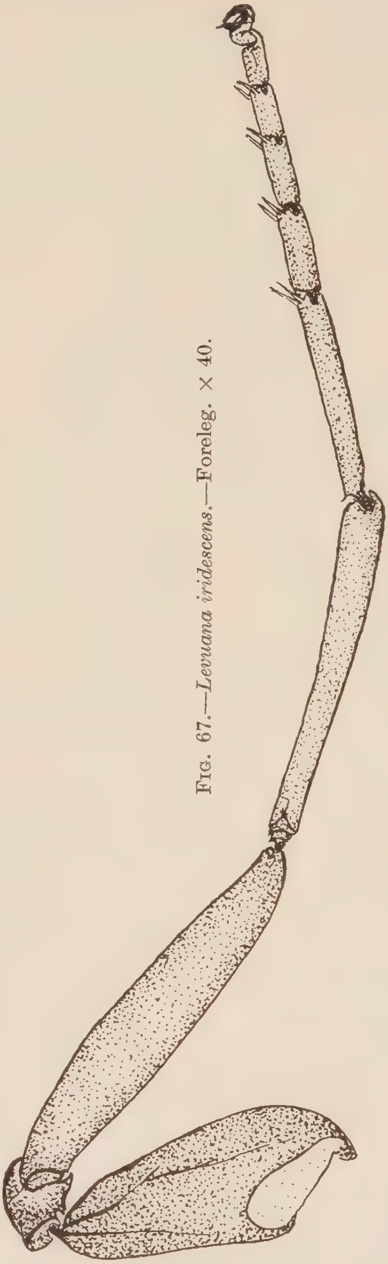

FIG. 67.—*Levuana iridescens.*—Foreleg. × 40.

The common occurrence of specimens in which that part of the wing normally tracheated by Cu_{1a} is actually tracheated by a third branch of M proves beyond doubt that M_3 and Cu_{1a} have fused together completely. Further, the fact that M_3 and Cu_{1a} are never present together in the same specimen (as Rs and M, for instance, are) implies that the complete fusion of M_3 and Cu_{1a} occurred at a relatively very remote period before M was appreciably approximated to Rs.

M_2 is the only trachea in this part of the wing which does not vary at all.

It is reasonable to assume that its constancy indicates that it is the only one not connected with the evolutionary changes which are in progress. M and M_1 will probably fuse completely with Rs in the course of time, but M_2 will remain separate.

It is important to realise that, despite this great variation of the pupal hindwing, the venation of the adult hindwing is always constant within small limits. The joint chitinisation of adjacent trachea to form single veins, and the development of subsidiary cross-veins to close the cell, are such that the arrangement of the veins in the adult wing is always the same, regardless of the variations of the preceding tracheae.

Conclusion.—The vein which is obviously lacking in the hindwing in M_3, and the vein which appears at first sight to be Cu_{1a} in its normal and primitive condition actually represents both Cu_{1a} and M_3.

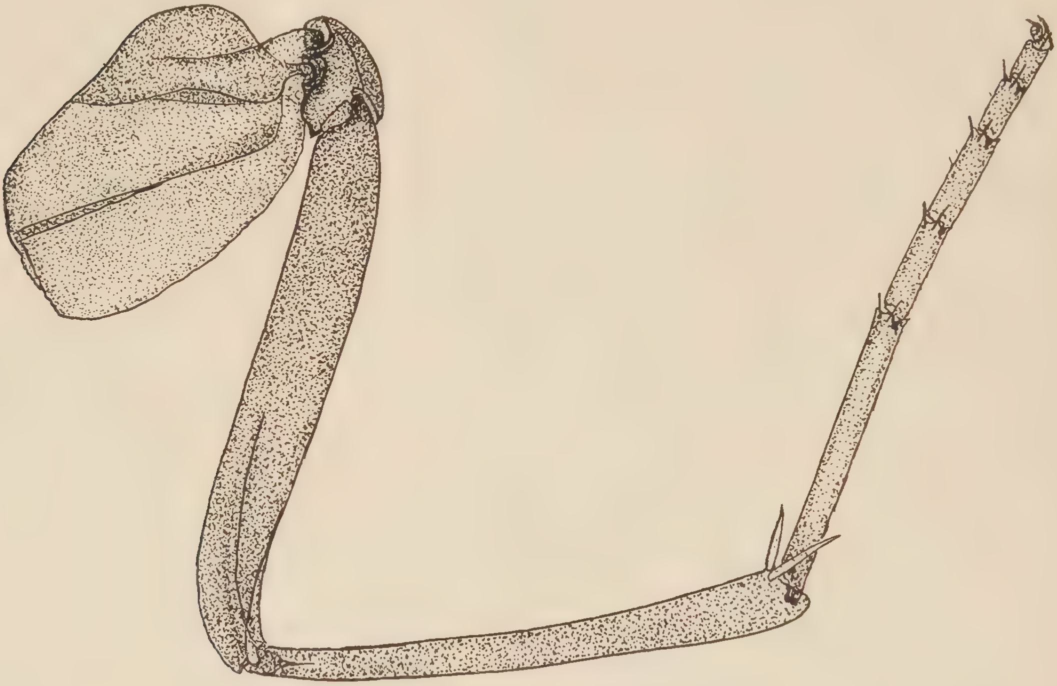

FIG. 68.—*Levuana iridescens.*—Middle leg. × 40.

Wing-coupling Apparatus.—A stout frenulum, consisting always of a single bristle, arises from a prominent humeral lobe at the base of the costa of the hindwing. At the base of the frenulum there are indications that this organ has been derived from three separate bristles that have fused together completely.

The retinaculum is of a very simple form in this sex. It consists simply of a particularly dense tuft of long curved scales which project forwards from the vicinity of vein Cu_1. The frenulum passes between these scales and the wing, but since the retinaculum consists of scales only, without any bristles, the frenulum is not held in place securely and is very easily displaced.

Legs (Figs. 67, 68, 69).—All the legs are of medium length and slender throughout. The middle legs are the longest. In the foreleg, the femur is a little longer than the tibia ; in the middle leg the femur and tibia are the same length ; and in the hindleg the tibia is longer than the femur. The tarsi are five-segmented and are longer than the tibia or the femur in all the legs. The first (basal) segment of the tarsus is in all cases more than twice as long as the second, and the third, fourth, and fifth segments are shorter than the second.

There is no trace of a spur or strigil on the fore-tibia. The middle and hind tibiae bear two short terminal spurs each. There are no middle spurs. In all the legs each segment of the tarsus, except the fifth, bears at its distal end two very short spurs. The fifth segment bears a pair of well-developed hooked claws.

Abdomen.—The abdomen is of the usual form, consisting essentially of ten segments of which nine and ten are fused together to form the external genitalia. Dorsally, the other eight segments are clearly defined, each having a well-chitinised tergite. Ventrally, only seven of them are apparent, the sternite of the first segment being greatly reduced and very closely associated with the metathoracic sternite. The external genitalia can be completely retracted into the eighth segment.

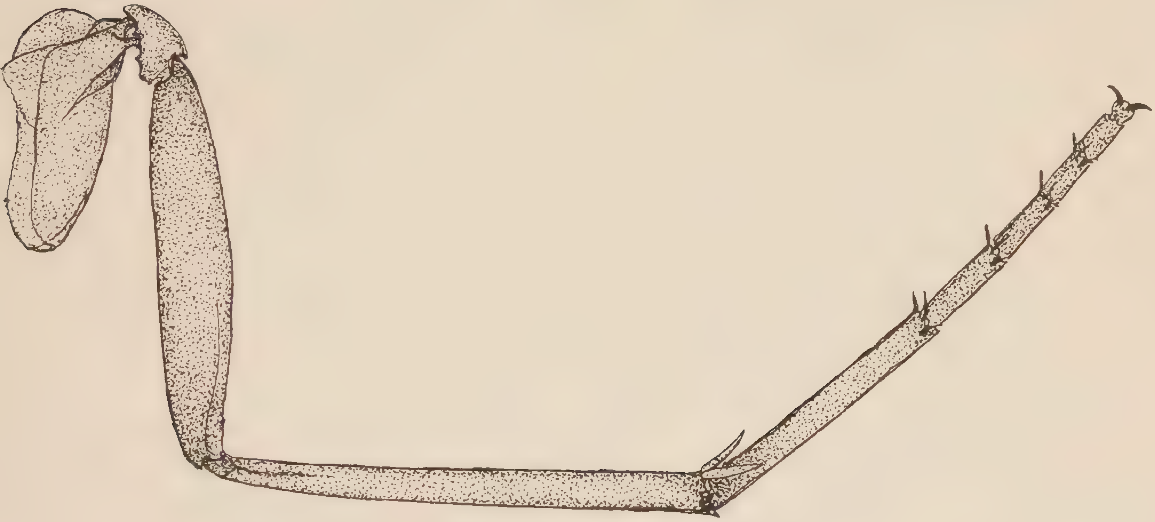

FIG. 69.—*Levuana iridescens.*—Hindleg. × 40.

The External Genitalia.—The external genitalia consist of a pair of thick convex lobes of characteristic shape (Fig. 70), which, when closed, completely surround the anus and the opening of the oviduct, both of which are terminal. Each lobe is densely covered with minute hairs and bears in addition many stout bristles. The opening of the bursa copulatrix is on segment 8.

The Internal Genitalia (Fig. 71).—The internal genitalia are normal in most respects. There are two ovaries, each of which consists of four ovarioles. Opening into the common oviduct there are five other organs. These are :

1. A long, tubular, accessory gland, which opens into the oviduct near the anterior end of the latter.
2. The seminal duct (from the bursa copulatrix), which opens into the oviduct nearly opposite the accessory gland.
3. The common duct from the two colleterial glands, which opens into the oviduct near its external aperture.

4 & 5. The paired accessory glands, which open independently into the uterus.

A small, thin-walled vesicle is connected by a separate slender duct with the seminal duct and is presumably the receptaculum seminis though its position is unusual.* Its duct joins the seminal duct near the bursa copulatrix. In the bursa copulatrix, near the internal opening of the duct which connects that organ with the exterior, there are two stout chitinous teeth.

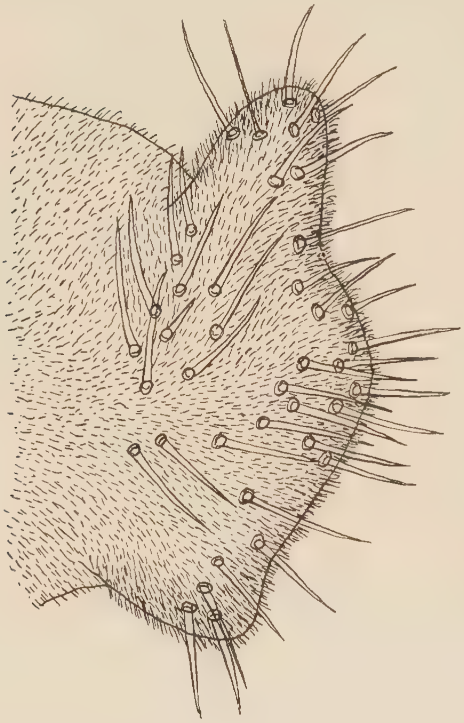
Fig. 70. — *Levuana iridescens.* — External genitalia of female. (Left lateral view.) × 200.

The colleterial glands are long tubes of uniform thickness throughout. They open separately into a large vesicle which is connected by a single, rather long, duct uterus.

Each ovariole may produce from two to seven eggs, the average being four. Numerous dissections of moths indicate that after the first batch of eggs is deposited no more of the egg rudiments in the ovaries mature. In such specimens, a decided discrepancy can always be seen in the ovarioles between any remaining fully-formed eggs and the adjacent egg rudiments (cf. Fig. 71, B).

Male.—The male differs from the female in the following respects only :

Head.—In the male the eyes are slightly larger (relatively) and are situated a little farther backwards.

Antennae.—The antennae of the male (Figs. 53, 54, 55, 56) are markedly different from those of the female. They are bipectinated throughout the length of the funicle, and the pectinations are long even on the basal segments, so that the antennae appear feathered rather than clubbed. The pectinations increase in length from the basal segment of the funicle to about two-thirds of the length of the funicle, and beyond this point they decrease in length.

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* The organ referred to at (1) above as an accessory gland was at first considered to be the receptaculum seminis, but in view of the appearance of the two organs in question it is far more likely that the vesicle is the receptaculum seminis.

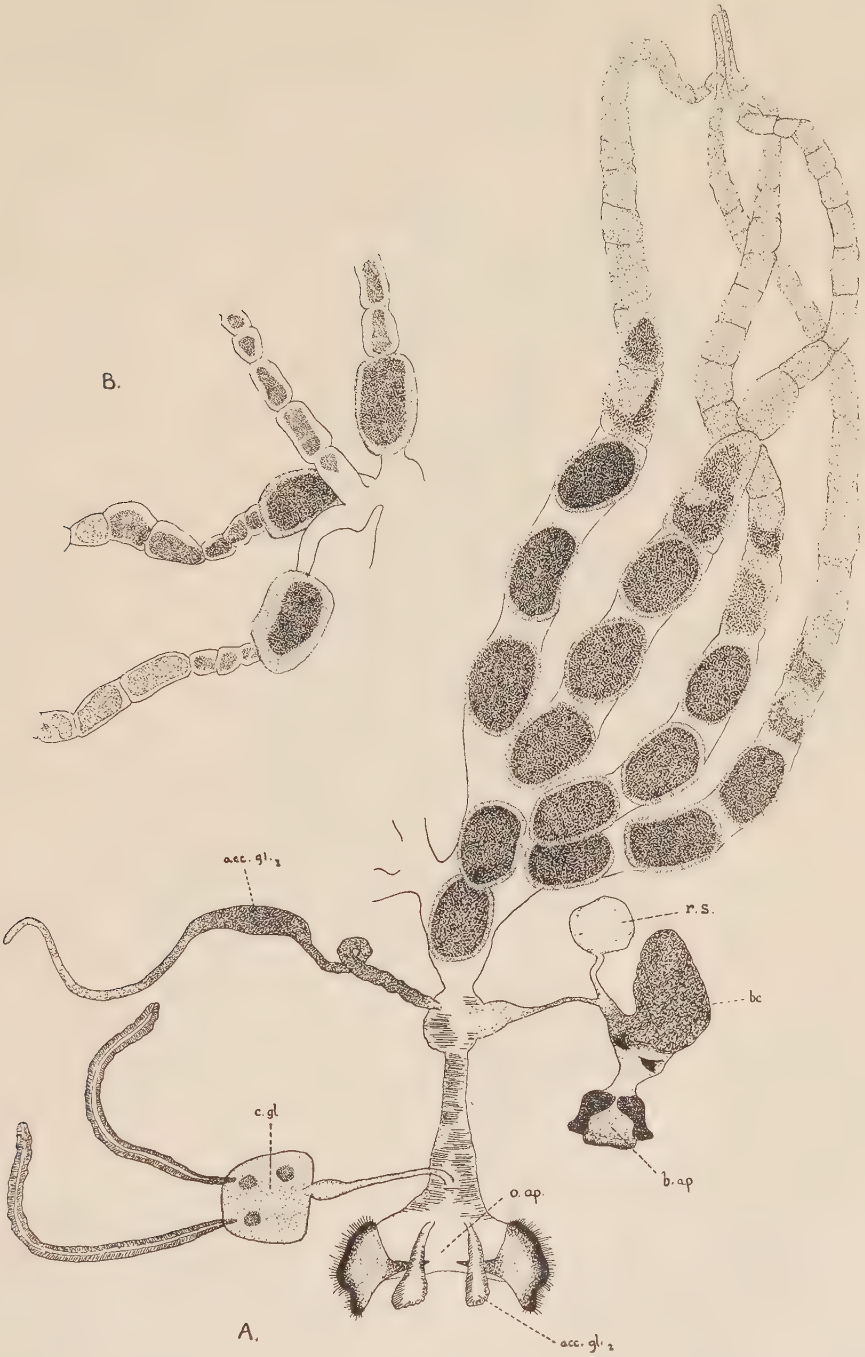

FIG. 71.—Female generative organs of *Levuana iridescens*. × 40. A. Moth killed just after starting to oviposit. Dorsal view, left ovary omitted. *acc.gl.*$_1$, first accessory gland; *acc.gl.*$_2$, second accessory gland; *b.ap.*, external aperture of bursa copulatrix; *b.c.*, bursa copulatrix; *c.gl.*, colleterial gland; *o.ap.*, external aperture of oviduct; *r.s.*, receptaculum seminis. B. Moth killed two days after laying the first cluster of eggs. Three fully formed eggs remain in the ovarioles; and the undeveloped egg rudiments occupy the remaining space.

They are covered with minute hairs, which are much more numerous than in the female.

The scape and pedicel, the terminal club, the funicular groove, and the relative lengths of the segments are the same in the male as in the female.

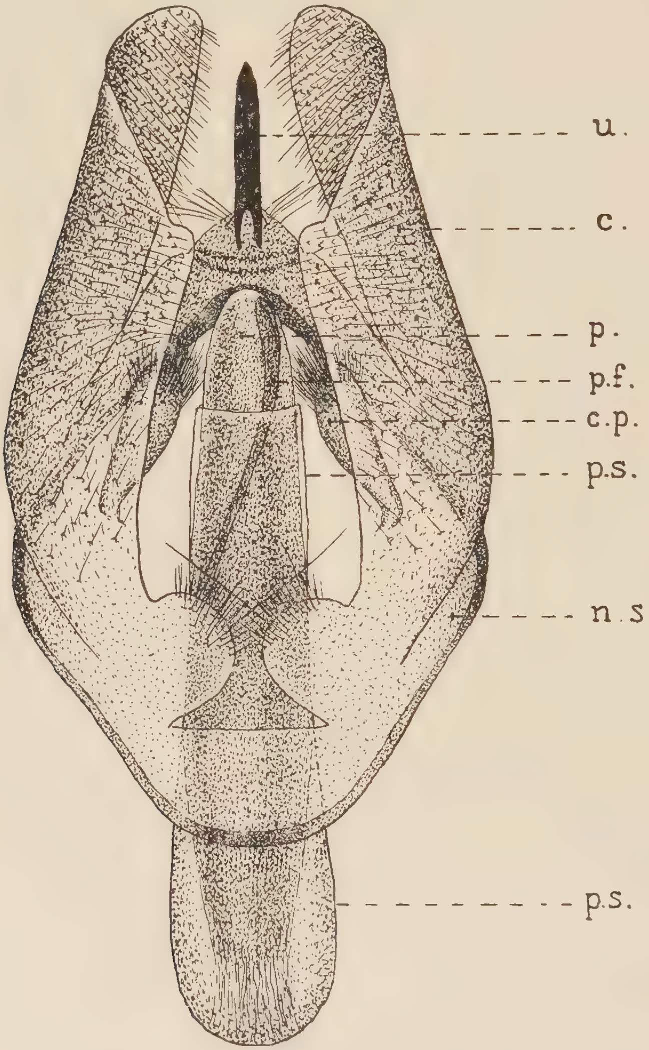

Fig. 72.—*Levuana iridescens.*—External genitalia of male. (Ventral view of cleared specimen.) × 100. *c.*, clasper; *c.p.*, strongly chitinised process arising from clasper; *n.s.*, exoskeleton of ninth abdominal segment; *p.*, penis; *p.f.*, penis-filum; *p.s.*, penis-sheath; *u.*, uncus.

The number of segments is also the same; that is, either seventeen or eighteen in the funicle and never more than nine in the club.

Thorax. Wing-coupling Apparatus.—The frenulum is the same as that of the female. The retinaculum, on the other hand, is much more highly developed and more efficient. It consists of a broad chitinous flap projecting backwards from vein Sc. Its free end strongly curved towards the wing membrane so as to form a kind of hook which holds the frenulum. It is very densely scaled.

Abdomen.—The abdomen is more slender in the male than in the female. The exoskeleton, apart from the external genitalia, is otherwise the same in both sexes.

External Genitalia (Figs. 72–73).—In all their more general features the external genitalia are of the usual Lepidopterous form. They are comparatively large and represent the ninth and tenth abdominal segment. They can be completely retracted into the eighth segment.

The ninth segment is in the form of a simple ring, strongly chitinised round its anterior edge. The uncus is hinged to it dorsally and is in the form of a long and very strong spike which is slightly curved downwards at its extremity. It is normally directed backwards but can be reflexed so as to point ventrally. Four or five setae arise from its base on either side. The anal opening lies on a large, soft, fleshy protuberance situated just below the uncus. There are no chitinous structures associated with this anal protuberance, the scaphium being absent. The claspers are large and simple in outline. They arise from the ventral half of the ninth segment and are curved so that they almost meet dorsally and ventrally. Their dorsal margins extend backwards and upwards almost to the level of the uncus so that they completely enclose the other organs. Each clasper bears at its base on the ventral aspect a flat, semicircular, chitinous lobe which projects towards the middle line and nearly meets its fellow of the other side. Each lobe bears many setae directed inwards and

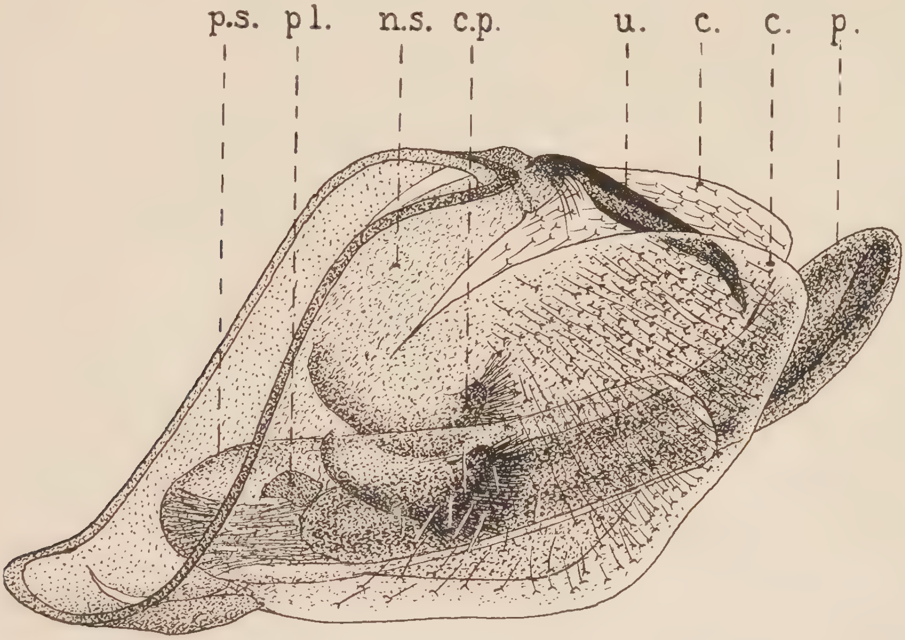

FIG. 73.—*Levuana iridescens.*—External genitalia of male (perspective dorso-lateral view of cleared specimen). × 100. *p.l.*, chitinous plate at base of penis. (Other lettering as in Fig. 72.)

backwards, one of which is much longer than the others. The two long setae cross one another in the middle line. The claspers are covered on their outer surfaces with ochreous scales, and on their inner surfaces, except basally, with short setae which are directed inwards and forwards. From the inner surface of each clasper near the basal end there arises, just below the mid-lateral line, a strongly chitinised rounded process which is directed backwards and bears distally a large number of stiff setae closely packed together. The penis is relatively large and is enclosed in a strong chitinous sheath which is broadly rounded at its anterior end. The ejaculatory duct enters the penis sheath on its dorsal surface and near its anterior end. The point at which the ejaculatory duct enters the penis is guarded inside the penis by a small, curved, chitinous plate of irregular outline and bearing many minute teeth. The penis-filum arises on the left side of the penis and curves across proximally to the right side. The saccus is wanting.

Internal Genitalia (Fig. 74).—The form of the internal genitalia is normal in most specimens. The testes are as a rule fused to form a single, compact, nearly spherical median, gonad completely enclosed by the scrotum. Each vas deferens is very wide for a short distance from the testis; it is then abruptly constricted, only to widen out again to form the vesicula seminalis. The two vasa deferentia are considerably swollen near their point of union, and these swollen portions receive the accessory glands.

Specimens occasionally occur in which the testis is lobular, consisting of two elongated, incompletely-fused lobes which are enclosed by the scrotum at their bases only. This may be a pathological state, and is certainly uncommon.

4. Proportion of Sexes.—Males and females occur in approximately equal numbers—although in certain broods there appears to be a preponderance of females. This was observed on the caged palm where in one brood the proportion of females to males was nearly 2 : 1. But in view of the fact that males in captivity died soon after mating for the first time, and that during outbreaks very few sterile eggs are laid, it seems likely that males must normally occur in as large numbers as females.

5. Habits.—A DIURNAL MOTH.—All the activities of the moth are carried on in the daylight. During the night they take up a resting position on the food-plant—often without seeking special shelter or concealment—and they are not easily disturbed. The best time to collect specimens is during the hour before sundown on a fine day when the moths are settled on the "vulu" and trunk of infested trees. At that time they are so unwilling to fly that they can be collected quite easily into tubes.

INFLUENCE OF LIGHT.—Although bright sunlight is usually avoided when selecting a place to settle, moths on the wing may remain fully exposed to the sun, and they are thus not completely shade loving. When kept in captivity, they always strive to reach the most illuminated part of their container. It is this habit which makes the breeding of *Levuana* in captivity so difficult. The only satisfactory method of so doing is to cage a palm in such a way that there is even illumination on every side. Otherwise moths on emergence make for the lightest part of the cage, and do not readily settle on the food-plant provided. Moths do not fly to a light at night.

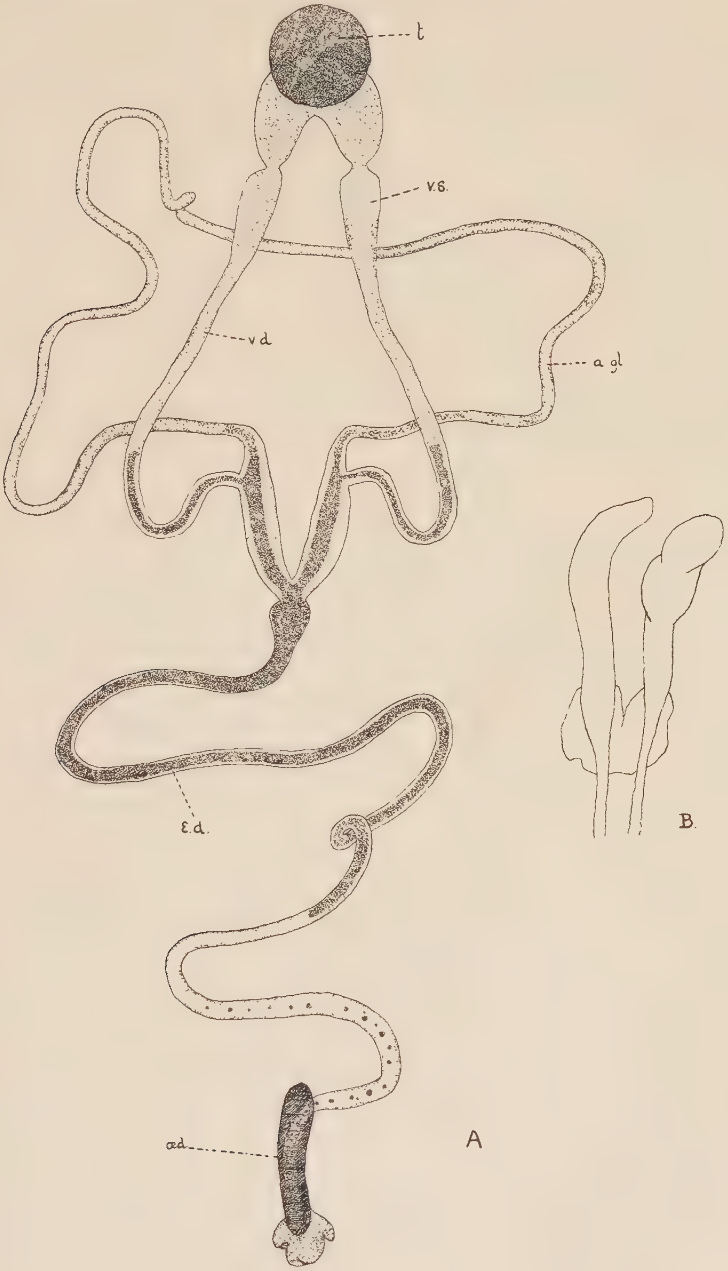

FIG. 74.—Male generative organs of *Levuana iridescens*. × 40. A. Typical form. *a.gl.*, accessory gland; *e.d.*, ejaculatory duct; *oed.*, oedeagus; *t.*, testes; *v.d.*, vas deferens; *v.s.*, vesicula seminalis. B. Testes of an abnormal form.

FLIGHT.—*Levuana* is not a strong flier, and it is seldom that moths remain on the wing for longer than five minutes. Under normal conditions of food abundance the flight of a moth is restricted to the immediate neighbourhood of its food-plant; and except when the males are flying about in search of unmated females, or when the latter are seeking leaves on which to oviposit, the bulk of the time is spent resting or crawling about the flowers of the food-plant. *Levuana* is quite unable to fly against a strong wind, and when such a wind occurs, numbers of them get blown away to leeward of the tree from which they emerged, the windward leaves of an exposed tree gaining comparative immunity from attack even in a bad outbreak. During a high wind, on the leeward side of an infested tree, moths may be seen in large numbers trying to fly into the wind, but being gradually blown back, except during a temporary lull, when they make slight headway.

The heaviest infestation ever seen has been on two trees which were each growing about 50 yards to leeward of an extensive outbreak.

The flight of the moth is very characteristic; the body is held almost vertical; the antennae project upwards and the wings vibrate with such rapidity that their colour is not displayed; so that the eye of an observer is temporarily bewildered by the sudden change in appearance of the insect as it settles.

When swarming in large numbers round their food-plant, their flight resembles that of a swarm of midges.

The maximum range of flight has not been accurately fixed. Experiments to test flying powers over water proved inconclusive owing to the difficulty of following such small, dark objects for more than 50 yards or so against the water. Several attempts were made to achieve this by liberating moths from a launch at a place marked by a moored dinghy, and following them as they flew over the water. But in no case was a moth followed for more than 100 yards, the majority of moths alighting on the surface of the water very shortly after leaving the launch, or else returning to settle on the launch. There was only a very slight breeze at the time.

Another test was carried out on different lines. Small coconut palms loaded with larvae of *Levuana* were kept on a launch anchored 150 yards to leeward of some heavily infected trees on the strandline limit of an extensive outbreak of the moth. Knowing the attraction which larvae have for moths when ready to oviposit, we thought that the latter might fly out to the launch from the shore. During four days, only one moth—a female—ever reached the launch, and that one flew over during a calm in the late afternoon.

Since we have several records, from studying the distribution of infested trees, which indicate flight of at least half a mile, the experiments described above were of little value.

The only way left open to us for determining the maximum flight range of the moth is by a consideration of the evidence derived from its distribution amongst the various islands around the coast of Vitilevu—the centre from which it spread.

Unfortunately it is not always possible to prove flight, as there is always the possibility of the moth becoming accidentally transported from island to island by human agency, although we incline to the view that this has not been so frequent an occurrence as some earlier workers have supposed.

We might, therefore, start by considering some of the islands within 15 miles of Vitilevu never reached by the moth and thus fix a minimum distance beyond which the moth is unable to migrate by unaided flight.

Levuana was on the east coast of Vitilevu for some fifty years at least without ever getting across to any of the Ovalau group which lies at a minimum distance of 6½ miles * in an easterly direction. The conditions prevalent near the end of outbreaks, *viz.* food shortage and swarms of moths on the wing, must have been reached time after time on the Vitilevu coastline, and had moths been able to fly 6½ miles without the assistance of the wind, which usually blows from the south-east, they would surely have reached the Ovalau group before 1922. On the other hand, an argument might be raised on the grounds that such a lengthy flight could only be accomplished in tranquil conditions or with a strong following wind ; and that such conditions, which can prevail on occasions during only six months of the year, did not happen to synchronise with the concluding stages of an extensive outbreak until after some forty years had elapsed since the first arrival of the moth in Fiji.

But in view of the fact that, as far as our observations go, *Levuana* is normally such a sluggish and weak-flying insect we favour the supposition that its arrival on Caqalai in 1922 was brought about by human agency. Similar evidence may be found in the case of Beqa, which lies 6½ miles to the south of Vitilevu, and where the moth was not reported till 1916. But this latter case is not so convincing, as no European lived on the island, and it is possible that *Levuana* may have arrived there farther back than 1916 and then died out, as it did on Malolo.

This seems to point to the fact that 6½ miles, unless down wind, is beyond the range of flight of the moth.

The moth never succeeded in spreading east of Ovalau, although Wakaya, the nearest island in that direction, is only 10 miles distant. This seems to prove definitely that the maximum range of flight is less than 10 miles.

When, however, we consider islands separated by less than 5 miles of open water from the nearest source of infection, we meet with somewhat conflicting evidence ; and the latter is often rendered inconclusive by the possibility of accidental human transportation. For this reason, island records of freedom are of more value than those of infestation. The most convincing of the former class are the small islands, Mubualau and Yagara (Stewart Island), which lie 2¼ miles E.N.E. and 1½ miles S.W. respectively of the nearest *Levuana*-infested land. In both cases the islands are fully exposed to the wind, and it is considered that they owe their escape from infestation to this fact.

On the other hand, the few definite flight records which we have been able to procure indicate that *Levuana* may cover a greater distance than is indicated by the evidence from the two last-named islands. Several instances have been met with on land where isolated coconut trees showing attack demanded a flight of nearly a mile. But the only absolutely definite flight-over-water record was that made by Mr. Simmonds in December 1922, when moths flew from Caqalai, a hitherto uninfested island, to Leleuvia, a distance of one mile over water in a southerly direction. There was, however, a fresh northerly wind blowing at the time. Several moths were found in the early morning on the launch anchored off Leleuvia, and on landing, more were found on the beach at the north side of the island. There is absolutely no doubt whatever that *Levuana* flew over in this instance.

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* All measurements over water in this account are in nautical miles.

There are several instances of islands becoming infested which would involve a flight of a few miles; but unfortunately we cannot claim them as providing absolute proof of unaided flight. The most convincing of these instances are the following:

(*a*) Leleuvia to Nagasautabu	2	miles	S.E.
(*b*) Malamala to Navini	3	,,	W.N.W.
(*c*) Navini to Malolo	3	,,	S.W.
(*d*) W. Vitilevu coast to nearest Yasawa Group island	4	,,	W. by S.
(*e*) Beqa to Yanuca	6	,,	W.
(*f*) Ovalau to Naigani	6¼	,,	N.W.

(The nearest source of infestation is mentioned first in each instance.)

The first of the above records is by far the most convincing record of flight, because Nagasautabu is only a small sandbank, less than an acre in extent, on which a few small coconut trees (not more than a year or so old) were growing at the time. Food shortage was complete on Leleuvia, the nearest land, and large numbers of moths must have been dispersing in all directions from its shores.

If this is a definite flight record, it is interesting that flight was against the prevailing wind; unless there happened to be a calm at the time, which is not an improbable occurrence for the time of the year (January) when the moth first appeared on the island.

On the other hand, although uninhabited, the small island is occasionally visited by natives on fishing expeditions, and they might have accidentally carried pupae or even moths from Leleuvia.

Similar arguments could be raised for and against the flight theory with any of the other islands mentioned in the above list. We favour the view that in most, if not all, cases infestation was caused by a flight, firstly, because *Levuana* is comparatively difficult to transport artificially without special arrangements being made; and secondly, because we know that under certain conditions at the end of an outbreak the moths do fly out over water in search of food.

Summary of Observations on Flight of the Moth.

1. *Levuana* is a weak flier and does not undergo long periods of uninterrupted flight unless driven away from the tree on which it emerged by strong wind or lack of foliage on which to oviposit.
2. The maximum distance over which *Levuana* is known to have flown is only one mile (over water).

3. There is inconclusive evidence that *Levuana* may on occasions have flown for as far as 6 miles over open water during certain favourable weather conditions.
4. Its maximum flight range is at any rate less than 10 miles, and it may be as little as one mile in localities where strong winds prevail.

FEEDING HABITS.—Both sexes have been seen feeding on certain flowers. Under experimental conditions moths show little or no attraction to sweet substances and do not readily feed; although when once they discover the food proffered they will take various foods, such as honey or sugar solutions of the cut blossoms of *Lantana* or "Mile-a-minute." In the field their most usual food is the nectar of coconut flowers, and it has been noticed that trees that have a spathe in flower at the time when moths are on the wind attract large numbers of moths.

Moths have also been seen feeding on the blossom of the following plants which in each instance were growing amongst or quite near to infested coconut trees:—

Mango.
"Mile-a-minute" (*Mikania scandens*).
Tournefortia argentea.
Lantana.
Ginger (plant with large yellow blossoms probably *Hedychium* sp.).

Probably this list could be added to considerably after further observation.

The proboscis is about ¼ in. long in both sexes and is not modified for any special function.

The taking of food does not seem to be essential to the welfare of the adult moth, since broods continue successively on small coconut trees which have not yet commenced to spathe and which occupy an isolated position in grassland. It is extremely unlikely that under such conditions moths leaving their larval food-plant in search of flower blossoms always manage to return to the same tree again.

ANTENNAL WAVING.—A very remarkable habit displayed by both sexes is the circular sweeping of the antennae after any movement or other physical exertion. The habit seems inexplicable because no specialised structure associated with the antennae has been discovered, and it seems to occur irrespective of any of those external stimuli to which the sensorial organs in the antennae might be expected to respond.

Although the habit is most pronounced in newly emerged moths, it has been observed in moths five days old, and it does not seem to cease altogether until a moth becomes so decrepit that it is incapable of any sustained physical effort.

The movement consists of circular sweeps of each antennae executed simultaneously. From the normal position of rest, directed forwards and slightly upwards, the two antennae move first towards each other, then downwards in the median line, outwards until they point in nearly opposite directions, and finally upwards again to complete the circuit. The maximum duration of the movement seems to be approximately thirty seconds in each sex, but when the antecedent exertion is only slight, the duration of the antennal waving is much less.

The movement dies out gradually by the " sweeps " becoming of less and less extent, and ends finally by one or two slight up-and-down movements of the antennae before the organs resume the position of rest.

The antennal movement never takes place until a moth has assumed the resting attitude ; it has never been observed when a moth is actually crawling or flying. It can readily be induced by causing a moth to move about, an action that always terminates with the phenomenon under discussion.

Emergence from Cocoon.—Emergence from the cocoon invariably takes place during the first few hours after dawn. Many moths die in their efforts to extricate themselves from a mass of pupae or from other débris that accumulates at the base of the leaves. The more fortunate ones crawl up the leaf stalk for a little way and then take up a suitable position where they rest for a few hours before flying away, during which time the wings expand and dry.

Wing expansion is a comparatively rapid process. Blood is pumped into the wings, and they swell more quickly and more visibly than a flat tyre when being pumped up. When inflated, they are folded together above the body in a vertical plane and kept thus for about five minutes, after which they take up the normal position of rest folded horizontally. The whole process is completed about ten minutes after emergence.

The two maxillae are meanwhile separated, and each is coiled and uncoiled separately. The latter action is continued for at least an hour before the proboscis is finally " assembled."

At the conclusion of each of the above described actions, violent antennal waving takes place.

Mating.—When moths are emerging in large numbers, mating usually takes place during the morning of emergence ; but a female may remain receptive for as long as four days, after which she soon dies if still infertile. A female when ready to mate adopts a characteristic attitude with the wings slightly parted and the abdomen exposed. To the latter is often imparted a quivering motion, the object of which may be to cause emission of an odour attractive to males. The latter fly in numbers around the locality where a receptive female is resting. As soon as a male moth locates the female the claspers are extended and it loses no time in commencing to mate. Other males often endeavour to mate with the same female, but the latter must very shortly cease to attract, because the less successful males soon disperse.

Males usually emerge before females in a brood, and so have to wait a day or two before mating ; but in captivity they will mate within six hours of emergence, so that a twenty-four hours' delay before mating is not a necessity for the full development of the gonads.

Mating seems to be a lengthy process ; and owing to the readiness with which moths in copula are disturbed it is not an easy matter to determine the limits of time within which the process may be completed. The only single instance in which a pair in copula were kept under observation the process lasted three and a quarter hours, starting at 6.45 a.m.

In captivity moths have often been observed to mate for a shorter time, but in several such instances the action was not completed, since the females, on dissection, were found to contain no spermatozoa in the bursa. We must conclude that several hours are required in order for the transference of sperm to be completed.

Mating usually takes place in the forenoon, although pairs have been seen in copula as late as 5 p.m. During an outbreak, moths in copula (cf. Plate XXIX) are a common sight on trees during the daylight hours.

OVIPOSITION.—Moths begin to oviposit on the day following emergence ; but in the few cases observed with moths kept in captivity oviposition has nearly always taken place on the second day after emergence. Moths that have failed to mate at the usual time generally lay infertile eggs on the third or fourth day after emergence and die immediately afterwards ; but fertilised moths, although they normally lay all their eggs at once, often live for a day or two.

Oviposition takes place at any time during the day. Having selected a suitable leaf on which to oviposit, a moth lays its eggs in a compact cluster on the leaf, taking about thirty seconds over the deposition of each egg.

The occurrence and arrangement of the egg clusters is described above (see under account of eggs), so the account will be confined to a description of those habits of the female moth which are concerned with oviposition.

Under normal conditions moths will continue to oviposit on the tree on which they spent their early stages until nearly all the leaves are defoliated. This condition would be reached after the fifth or sixth generation on a full-grown tree previous to the introduction of *Ptychomyia ;* the final brood, which would be the largest from the point of numbers, would have the least available leaf surface on which to oviposit. So that at the conclusion of an outbreak a tremendous concentration of eggs would result. The following instances are interesting in this respect.

On an isolated tree near an extensive outbreak on the Ra coast in June 1925, eggs were laid on 76 out of 162 leaflets of one leaf. There were altogether 121 clusters totalling some 3,000 eggs. In addition to these there were just as many small larvae feeding. But an even more extreme case of congestion was met with at Naigani in November 1925, where an extensive outbreak had almost completely defoliated every coconut tree on the island. A count was made of the eggs laid on the newest leaves of a 20-ft. tree. On the central leaf, only eighty leaflets—*i.e.* approximately one-third of the leaf surface—of which were expanded, there were no less than 311 egg-masses. About 10 per cent. of these masses were laid on the upper surface of the leaf. Only fourteen leaflets were without eggs, and on one small leaflet there were no less than twelve egg-masses (about 350 eggs). This means that upwards of 10,000 eggs may be laid on a newly opened leaf towards the end of a bad outbreak.

One of the most striking things about the appearance of fairly recently infested country is the way in which individual trees are heavily defoliated whilst neighbouring trees are still green. Not until one tree becomes so congested that there is little room available for further oviposition do the moths abandon it and seek fresh foliage on neighbouring trees; but true migration in the sense applicable to many Lepidoptera never occurs, although at the end of an outbreak when defoliation is approaching completion over a considerable area, moths fly for a comparatively long distance to discover unattacked trees on which to oviposit; they do not, however, fly in a swarm in any definite direction, but scatter in all directions in calm weather, or else get blown down wind.

Moths when ready to oviposit seem to be attracted in some manner by their larvae; and we have ample proof that the presence of larvae has caused moths to oviposit on leaves that they would otherwise not have visited.

During the winter of 1925 the small previously uninfested palms which we loaded with larvae for spraying experiments in Suva were shortly afterwards visited by moths from a distance, and these laid eggs only on those leaves on which larvae were feeding. But the most convincing proof of this larval attraction for moths was found during an examination of an extensive outbreak at Nanuku estate on the north coast of Vitilevu. Here on a small piece of land less than an acre in extent, which had been planted up as a native garden, were growing coconuts—high and low trees—bananas, maize, rice and sugar cane. The site had been abandoned as a garden for some six months, and the crops mentioned had grown lank and were crowded together (Plate XXI, Fig. A). *Levuana,* which had swept through the whole plantation in the early months of 1925, had by June become well established on the smaller coconut trees. Two of these small trees growing in this derelict garden were so crowded with larvae, when the site was first visited, that the latter had dropped off on to leaves of some of the other plants, on which they were now feeding. Several larvae were found on a banana leaf, a few were also feeding on rice and sugar cane. A week later the site was revisited. Moths had been emerging in large numbers in the interval, and a careful search was made for eggs. The central leaf of the coconut, not yet completely unfurled, was in each case plastered with egg masses; but it was very interesting that an occasional egg-mass had also been laid near to the larvae which were feeding on the leaves of bananas and sugar cane. The fate of the larvae, which hatched out on these unusually attacked plants, was watched carefully, and although a few of the newly hatched larvae managed to feed on the banana leaf, none of those which hatched on the sugar cane were able to gnaw through the tough epidermis of the leaves, and all of them died. So that in the case just described *Levuana* oviposited on a plant on which its larvae (the young stages at any rate) were unable to feed, the only apparent reason for which was that it was attracted to the plant by larvae which had accidentally fallen on to it.

When forced by food shortage to fly to unattacked trees, *Levuana* always selects the highest trees first on which to oviposit, and it is not till several generations have bred that the moth descends on to lower trees; seedlings and trees with no trunk do not become attacked until the concluding stages of an outbreak.

Levuana always oviposits on the newly opened leaves and then works downwards as the top leaves become defoliated. Just the opposite habit is displayed by *Artona catoxantha*, which apparently always lays on the bottom leaves first. Thus by examining the defoliation of a tree leaf by leaf, it is possible during the earlier stages of attack to tell whether the moth has been breeding on the tree continuously or whether it has only just recently attacked it, with or without signs of a previous attack still evident on the oldest leaves. (See Plate XX.)

Reaction to Climate.—(*a*) *Rain* has little effect on adult moths except that it curtails their activities on the wing and they rest in shelter under the leaves or " vulu " on the leeward side of a tree. They are very unwilling to settle on a wet surface, and a moth kept under mosquito netting fully exposed to the rain would not settle for long anywhere, but kept flying about unable to find a dry place on which to rest. But rain very seldom falls continuously for more than twenty-four hours, and even when it does, it would only very rarely synchronise with a period of moth emergence. Short, heavy rain storms which are of more frequent occurrence would not damage the moths, owing to the very complete shelter available under the leaves of a coconut tree. It therefore seems very unlikely that rain in any way inhibits the normal activities of the adult moth

(*b*) *Cold.*—We have not tried keeping moths at a low temperature ; but they survive without harm the comparatively low temperatures (± 55° F.) reached at night in the dry zone of Vitilevu during the winter months.

(*c*) *Wind* has a very decided influence on the behaviour of adult moths. In view of their inability to fly against even a moderate wind, it is not surprising that on trees exposed to the full force of the wind they only oviposit on leaves whose under surface offers some degree of protection. Thus the defoliation of such trees becomes very irregular, and at Nanuku plantation, where *Levuana* completely defoliated acres of small trees, tall trees which acted as a windbreak were hardly touched.

CONTROL OF LEVUANA IN FIJI BEFORE 1926

Under this title we propose to discuss those factors which contributed towards control of *Levuana* in Fiji both during its outbreak phase and intermediate periods of comparative scarcity.

At certain periods and in certain localities, the moth increased to such an extent that those factors that are ordinarily classed as factors of natural control had no appreciable effect in reducing the number of the moth.

We might, therefore, classify the rather broad range of subjects which we propose to consider under three headings :—

1. Factors that are responsible for the termination of outbreaks.
2. Factors that cause a certain degree of immunity to the coconut crop by limiting the dispersal of the moth.
3. Factors that are always acting to the detriment of the moth, but which only have economic value when and where *Levuana* is in small numbers.

But as several of the factors under consideration might justifiably be included under more than one of the three headings just enumerated, it seems more reasonable to treat each one separately, pointing out its particular control value in the *Levuana* position as a whole.

Listed in their probable order of importance, these factors are as follows :—

1. Limitation of food supply.
2. Suicidal habits of the moth.
3. Geographical barriers.
4. Climatic influences.
5. Predators.
6. Abnormal mortality in young larvae.
7. Fungi.
8. Infertile eggs.
9. Parasites.

These factors all interact in natural surroundings and may help to retard the rapidity of increase of the moth.

During preliminary experiments to test the use of arsenical sprays on *Levuana* in Suva during 1925, we were struck by the comparatively high mortality that occurred during the early stages of a brood.

We loaded certain trees with egg masses and made subsequent daily counts of the number of larvae on each of the leaves. Only a percentage, ranging from 0 to 80, of those individuals originally placed on a tree reached maturity.

It is quite obvious that were the mortality always as high as it often was during these experiments, *Levuana* would never become a serious pest. But the anomaly is explained by the fact that all of the factors concerned in control do not always react at a maximum in the same place and at the same time ; and that when once *Levuana* has increased in any area beyond a certain critical concentration, one lot of controlling factors drops out, with the result that the moth increases with sufficient rapidity to cause an outbreak of economic importance.

Exactly when that critical concentration point is reached it is not possible to state by so many numerical data, but we think that concentration of food supply is an all-important factor in determining potential outbreak areas, within which the critical concentration point of *Levuana* is generally exceeded. Once an outbreak starts, surrounding areas, where there is a less concentrated food supply, may rapidly become infested.

1. Limitation of Food Supply.—There must be very few Lepidopterous pests that are able to defoliate trees over an extensive area as completely and rapidly as did *Levuana* before it was controlled by introduced parasites ; and yet there is not the slightest doubt that *Levuana* outbreaks were in the majority of cases terminated primarily by the complete exhaustion of the food supply over a circumscribed area of infestation.

The fact becomes more readily understandable when it is remembered that without any effective natural enemies the numbers of moths increased with astounding rapidity during each brood. Increase in the number of individuals meant increase in the rapidity of defoliation, accompanied by decrease in the size of the newly formed leaves and in their rate of output.

These factors all combined to make the concluding stages of defoliation extraordinarily rapid, until progress became suddenly stopped by the starvation within the area of the majority of the insects.

Each *Levuana* larva requires about 3 square inches of leaf surface as food during its entire development.

Each leaflet of a coconut tree has an average underside surface area of about 30 square inches. In order to render a leaf completely useless for a further supply of larval food it is necessary for only 44 per cent. of the leaf surface to be consumed by caterpillars—the remaining portion between the feeding scars soon rotting and withering.

An average leaf with 200 leaflets (a fairly liberal estimate for a tree subjected to *Levuana* attack) would thus have $30 \times 200 \times \frac{44}{100}$ or 2,640 square inches of leaf surface available for larval food ; that means sufficient to enable 880 larvae to feed entirely on one leaf.

Owing to the normal mortality from various causes amongst eggs and larvae during their development, a proportion of the leaf becomes eaten away by larvae which never mature ; so that rather less than 880 maturing larvae would be sufficient to cause complete defoliation ; the exact number varying in accordance with the degree of concentration of controlling factors in any one locality. But as most of the food is eaten by larvae in the last two instars, the numerical reduction would not be so great as one might expect from the number of individuals that die before the third moult. Therefore, we may say that each leaf will provide food enough for 800 larvae to reach maturity.

An excellent opportunity for an investigation of the food shortage factor was presented by the concluding stages of the 1925 outbreak on Naigani.

When the island was visited in November of that year, the trees all over the island, which formed a single outbreak zone, were almost completely defoliated (cf. Plate IX, Fig. C). Four trees, representing as nearly as possible the average condition for the whole area, were cut down and examined leaf by leaf. The percentage defoliation of each leaf was computed, and a conservative estimate of the number of eggs and larvae present on each leaf was made. Fig. 75 shows a graph of the average percentage of available larval food remaining on the leaves (total nineteen) of the four trees examined.

This graph, therefore, represents the state of defoliation of an average tree on Naigani in November 1925. If the remaining leaf foliage on each leaf of this average tree be summed up, it will amount to 257 per cent., or the equivalent of two and a half completely healthy leaves.

We have established above that one healthy leaf will provide enough food for 800 larvae to mature ; therefore, the average tree on Naigani at this time had only enough foliage left to support 2,000 larvae ; whereas actually there was an average number per tree of 7,717 eggs and 6,450 larvae—making a total of 14,167 individuals.

It is therefore evident that on most trees on the island only about 15 per cent. of the *Levuana* present would pupate, leaving a larval starvation mortality amounting to about 85 per cent.

Defoliation at this stage would become so rapid that by the time moths

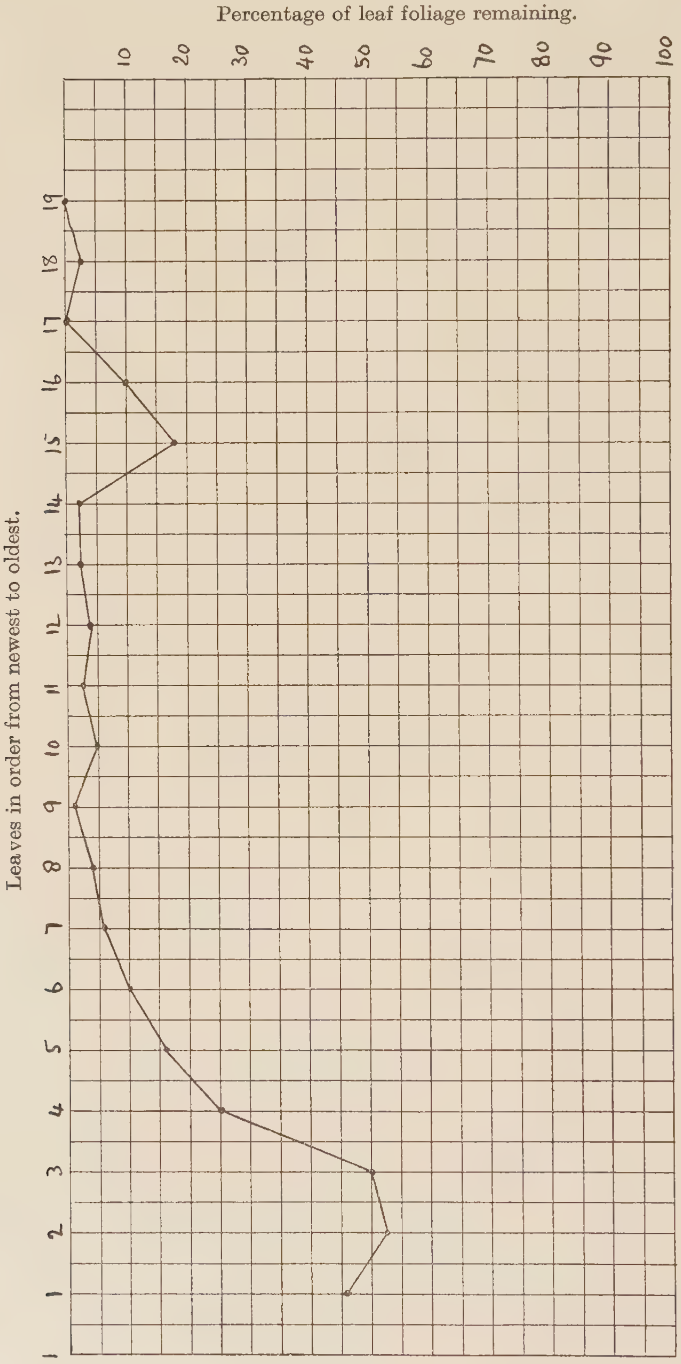


Fig. 75.—Damage done to the leaves of four coconut trees by *Levuana* larvae representing average defoliation on the island of Naigani in November 1925.

emerged there would be practically no foliage available for oviposition, resulting in the preoviposition death of most of the moths.

A reinspection of the island in March 1926 showed that the results figured out above actually took place.

Levuana was found in quite small numbers on an occasional tree; and all the trees which had not died as the result of repeated attacks had by then put out two or three stunted green leaves above a mass of completely dead foliage.

It must be stated that although *Ptychomyia* had been liberated on the island at the time of the first visit in November, examination of old pupal masses in March showed that it had not become numerous enough to play any part in bringing the outbreak of *Levuana* to a close.

Outbreaks, such as that on Naigani just discussed, were of very general occurrence throughout much of the *Levuana* belt up till the end of 1925, and although inspections were not always coincident with their concluding stages, there is little doubt that in a great many cases their abrupt termination was brought about by starvation of the moth.

2. Suicidal Habits of Levuana.—In spite of the contradictory views of some later observers, there is no question that Knowles was perfectly right when he stated (*loc. cit.*) that " undoubtedly many moths are prevented from emerging by the mass of cocoons above their own." It has already been pointed out that prepupae habitually tend to spin their cocoons one on top of another until a mass of pupae three or four deep is found. Amongst the lower layers of any such pupal mass will always be found dead pupae whose appearance is most characteristic (cf. Plate XXVIII) and leaves no room for doubt that they died in their efforts to push through other cocoons.

There is abundant evidence to show that this habit of cocoon massing, with its resulting high mortality amongst the pupae, was, next to completion of food supply, the most important cause of the more or less rapid termination of *Levuana* outbreaks prior to 1925. Actually the most convincing proof of the importance of pupal massing as a factor in control was obtained on Makuluva in January 1928, where *Levuana* had been abundant, in spite of the presence of *P. remota,* for more than two years. The following is a short summary of the circumstances :—

The locality was visited in December 1927; the bulk of individuals were in the last two larval instars, and many had already pupated. A large number of pupae were collected from one tree for purposes of photography, and nothing unusual was noticed in their condition except that they were formed up in particularly large masses.

Practically every tree on the leeward side of the island had a heavy infestation of the moth at this time. Although the food supply was nearly exhausted on certain trees, others had quite a number of green leaves still remaining. The parasitism was only 15 per cent. in the pupae.

Three weeks later the locality was revisited. A striking change had occurred. Only eight fifth-instar larvae were found, and there were large masses of pupae very few of which had given rise to adults. An examination of the numerous pupal masses showed that the bulk of the pupae which had died were mature and had the distorted appearance of pupae that had died during their struggles to emerge. An unusual factor was that the surface layer of pupae had yielded fewer moths than is usual; but here again death had occurred after the pupae had matured, and was presumably caused by mechanical factors. At this time only three trees could be found with *Levuana* still alive on them. Very few eggs were found, and many of these were infertile.

A careful calculation of the parasitism in the dead pupal masses gave a percentage varying from 15 to 50 on different trees, the former figure being the most usual.

Only very few of the dead pupae had signs of fungus in them, and there was no sign of the mite, *Pediculoides ventricosus*. There had been nothing unusual about the climatic conditions since the island was visited three weeks before.

We must conclude from this that the tremendous decimation of the *Levuana* brood, which had quite obviously occurred during the pupal period, was due to the inability of a very large percentage of the moths to emerge from the cocoons, owing to the extremely massed condition of the latter.

Prior to this very clear-cut instance of the suicidal nature of the pupal massing habit, it had been very difficult to arrive at any accurate estimate of the percentage of deaths from this cause.

Owing to the large number of scavenging insects, principally ants, present in the crown of a coconut tree, and the effects of wind and rain, it was almost hopeless to try to compute the percentage of moths which had died as the result of overcrowding of pupae.

At Yanuthalailai in November 1925 we examined a number of last brood pupal masses and made the following mortality counts :—

In masses with less than 10 pupae, mortality averaged 11·8 per cent.
,, ,, ,, 10 to 50 ,, ,, ,, 29 ,, ,,
,, ,, ,, more than 50 ,, ,, ,, 37·8 ,, ,,

The mortality in each instance refers solely to that caused by failure of the moths to force their way to the surface of the mass.

These figures would not be high enough, with the additional effect of other factors, to cause a diminution in the numbers of the successive broods; but then *Levuana* was not particularly numerous on Yanuthalailai at the time; moreover, the trees had a large number of leaves which offered a greater available space for pupation.

Another estimate of pupal massing mortality was made on Naigani in November 1925, when an extensive outbreak was in process of "cleaning up." The pupal masses from a typical tree were all examined, and 1498 had yielded moths and 1651 contained dead mature pupae, the percentage mortality in this instance being 52 per cent. Here again the figure would not be high enough to cause cessation of the outbreak. But the available food on the island was finished about the time the count was made and, as has been stated already, food shortage was the primary cause of the subsequent clean-up right over the island.

We therefore have arrived at the conclusion that the particular factor

PLATE V

"CARRY OVER" TREES ON YANUTHALAILAI

under discussion does not influence the initial broods of *Levuana* in a locality at all, but that after a number (perhaps six or seven) of broods have fed in one locality, causing a weakening of the trees and a slower output of leaves, the available space for pupation diminishes as the numbers of the moth increase, until finally a stage is reached in which all but a small percentage die as pupae. If the food shortage condition is reached prior to this stage, the outbreak will terminate before the pupal massing factor plays any important part.

3. Geographical Barriers to Distribution.—It is doubtful whether any configuration of the land area in Fiji has ever been responsible for checking the spread of the moth throughout a district where coconut trees or other food plants are generally distributed.

The altitudinal range of the moth in Fiji seems to coincide with that for the coconut palm and for the "Niu Sawa."

Outbreaks of the moth were of fairly common occurrence in rather isolated belts of coconuts far up the river valleys in the centre of Vitilevu at an estimated height of a thousand feet above sea-level; but there were no long flights involved to reach such places.

On the other hand, coconut trees growing at an elevation of 2,700 feet at Lewa in Colo North Province of Vitilevu were free from all past or present traces of the moth, when examined in 1925, but around there was a considerable belt of country—at least five miles—devoid of coconut trees, which would almost certainly be the cause of the failure of the moth to spread to this and other such places.

On the north coast of Ovalau *Levuana* reached a grove of Niu Sawa palms in the bush at 1,100 feet above sea-level, but here there was no great flight involved as the palms were only a mile from a thick coastal belt of coconuts a few of which extended back into the bush.

As probably 90 per cent. of the available food supply for the moth lies on the coastal plains of the islands, we can eliminate land configuration as a factor in limiting the distribution of the moth.

The extent to which water is a barrier to the distribution of *Levuana* depends entirely on the flying powers of the moth, and it has been almost impossible to form any rigid conclusions as to the extent of water required to prevent dispersal of the insect by unaided flight. The evidence which we discuss at length elsewhere (p. 137) leads one to believe that the moth is incapable of a flight of more than about two miles over water, and that where its occurrence on an island involves a greater distance transportation has been by human agency or by hurricanes.

4. Climatic Factors.—*Rain.*—After exceptionally heavy rain, the pupal masses at the base of the leaves become very sodden and several cocoons get washed off and the pupae killed; but this is of comparatively rare occurrence.

Adult moths shelter beneath the leaves and are not affected by rain. Larvae and eggs are always protected more or less from rain by their position under the leaves, and even larvae feeding on a newly opened leaf, which catches a certain amount of rain on the under surface, do not seem to take any ill effects from the exposure.

Whereas *Levuana* thrives best under moderately humid conditions, there is no evidence to show that the almost annual drought during the winter months on the leeward side of Vitilevu is the cause of the comparative freedom from the pest of many localities, in that outbreaks have progressed without a break in the dry zone for sometimes as long as two years.

Wind.—Wind has a more far-reaching effect than rain on the *Levuana* moth. The adult moth is a weak flier and is unable to breed on trees which are permanently exposed to high winds. The localizing effect of wind is well marked in many localities, amongst which the following are some striking instances :—

1. *Levuana* never succeeded in flying to Yagara, a small island lying 1½ miles to windward of Beqa.
2. On Makuluva, where an outbreak was in progress for nearly two years, the trees on the leeward side of the island were heavily infested and at times almost completely defoliated ; whereas to windward the trees remained entirely free from the moth for the bulk of the time.
3. On individual trees growing in a wind-exposed area on Nukulevu—a small island off the east coast of Vitilevu—*Levuana* bred on those leaves which projected from the lee side of the tree and never oviposited on the more exposed leaves. One tree in particular had the following interesting defoliation record when it was cut down in April 1926 :—

Leaves in order from the youngest.	Per cent. defoliation by *Levuana*.
1	0
2	0
3	0
4	2
5	2
6	1
7	55
8	0
9	35
10	0
11	2
12	0
13	5
14	65
15	5
16	0
17	55

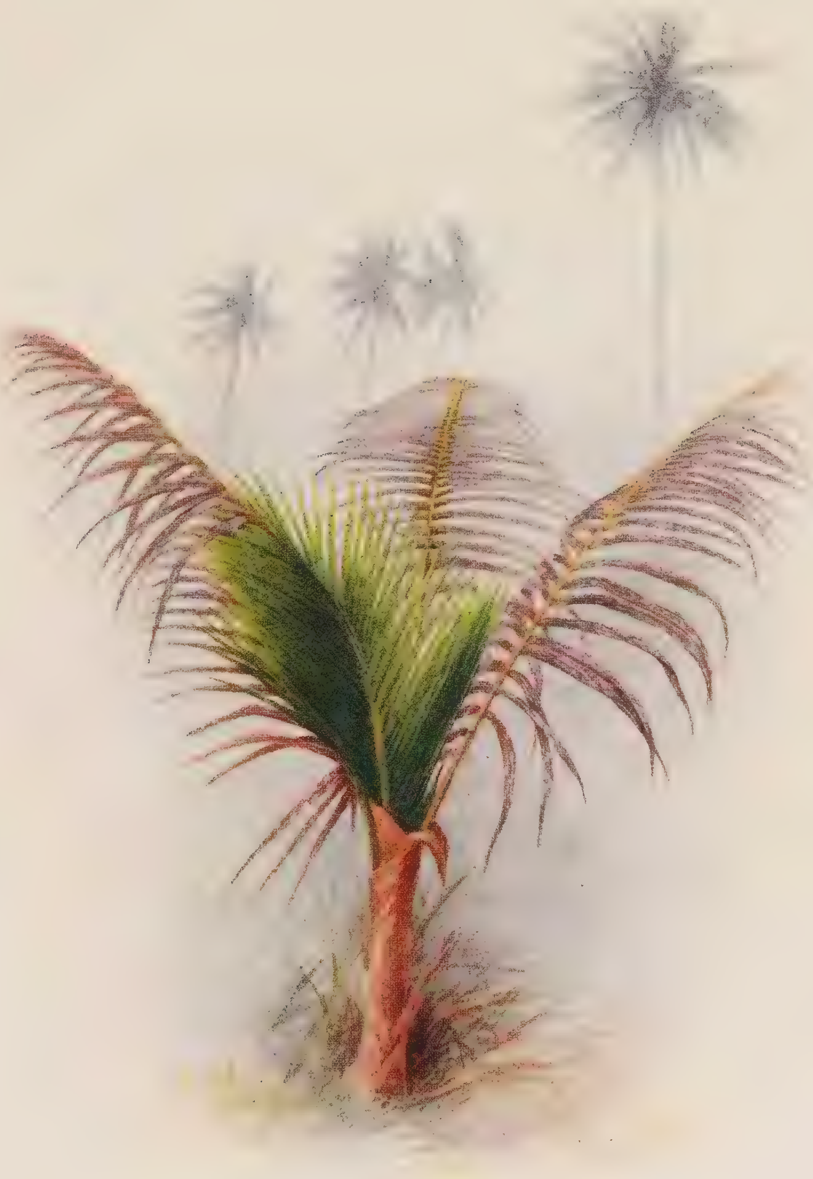
These three examples, which illustrate immunity of an island, immunity of trees on the windward aspect of an island, and lastly immunity of leaves to windward of an exposed tree, all show that wind can and does play a rather important part in limiting attacks of the moth. Occasionally heavily infested areas are met with fully exposed to the wind, such as the coastal strip of Moturiki between Daku and Naicabicabi. But here the trees are growing so close together that moths managed to find their way even to those trees on the most exposed portion of the shore.

PLATE VI

THE EFFECT OF WIND IN THE LOCAL DISTRIBUTION OF *LEVUANA*

One of several isolated young palms on the leeward side of the island of Makuluva showing heavy defoliation by *Levuana*. It was frequently supplied with moths carried by the S.E. trade wind from the centre and windward side of the island. Such palms in exposed situations on the windward side of islands were generally immune from attack.

PLATE VI



Wind also causes a certain amount of damage to the early stages. Pupal masses formed right down at the base of the leaf stalk become squashed when the leaf is pressed by the wind against the crown of the tree. Larvae feeding in the centre of a leaflet often meet with the same fate; and eggs and larvae get brushed off by one leaf rubbing against another. But, apart from limitation of flight, the total damage caused to the moth by climatic factors is small, and only helps in control during those times when the moth is scarce.

5. Predators.—The total control of *Levuana* exercised by predators was quite insignificant during outbreaks; but when the moth was reduced to comparatively small numbers by food shortage, the predators, which had increased in numbers during an outbreak, played an important part locally in killing off the few remaining moths left on certain trees. Not one of the insects that from time to time have been seen feeding on *Levuana* is monophagus. With the exception of an ubiquitous Attid spider and certain species of ants, they are all comparatively rare insects on coconut trees when *Levuana* is not present.

The following is a list of all the predators observed by us or by previous workers in Fiji, exclusive of insects introduced expressly to control the moth since 1924. Altogether seventeen different species of probable predators have been noted, but only twelve of these can be claimed as definitely predacious on the moth, of which probably not more than seven are of any importance in its control.

Reptilia.	Lizards.
Aves.	Domestic fowl.
	*Bulbul (*Molpastes fuscus*).
	*Mynah.
Arachnida.	*Ascyltus pterygodes*, Koch.
	Pediculoides ventricosus, Newp.
Insecta.	*Tapinoma melanocephalum*, F.
	Tetramorium guineense, F.
	Pheidole megacephala, F.
	Paratrechina (*Nylanderia*) *vividula*, Nyl.
	**Polistes macaënsis*, F.
	Cantheconidea cyanacantha, Stål.
	Platynopus melanacanthus, Boisd.
	Oechalia consocialis, Boisd.
	Tectocoris lineola, F.
	**Anisorcus affinis*, Crotch.
	**Chelisoches morio*, F

LIZARDS.—There are several species of lizards that frequent coconut trees in Fiji; in fact, one rarely examines a tree without finding at least one lizard—often on the central leaf—where they frequently hide between partly unopened leaflets. At least one species lays its eggs on coconut trees. In view of their abundance, and the fact that whilst studying an outbreak of the moth for five consecutive weeks we never noted a single instance of a lizard attacking a moth, it seems very unlikely that they feed on *Levuana* to any extent. Two specimens of a small undetermined species very common on coconut trees were collected from a tree well infested with *Levuana* in Suva in 1925 ; their stomachs contained no trace of *Levuana*, the contents consisting mostly of small Orthoptera and Tineid moths.

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* Predatory records doubtful.

The only record we have of a lizard attacking *Levuana* was made by McNamara, who saw an adult moth eaten by a small lizard inside the large wire breeding cage in Suva. He did not collect the lizard, so we do not know the species. Since the small Locustids on which these lizards seem mostly to feed do not get inside the breeding cage, it is possible that lizards were driven to resort to a less customary diet when living on the caged-in tree.

Birds.—A popular belief existed amongst certain planters that, after the introduction to Fiji of the Indian Mynah bird, the native birds, which had supposedly been keeping the *Levuana* moth in check, were driven out of plantations, with the result that the moth became a pest. Furthermore, the likelihood of bird control being operative on certain islands not known to be infested by the moth was suggested in the writings of some of the early workers on *Levuana* in Fiji.

But since *Levuana*, belonging to a family of moths known to be distasteful to birds, was refused when fed in captivity to two exclusively insectivorous birds (Drongo and Magpie Robin) brought from India with a view to assisting control of the moth, there seems no justification for thinking that native birds ever played any part in the control of *Levuana ;* and it is not surprising that so few instances of the moth being attacked by birds have been met with in Fiji.

Knowles (*loc. cit.*) in 1918 saw a bird of unknown identity " searching under the leaflets of a coconut palm badly attacked by *Levuana* " ; he concluded that it was feeding on *Levuana* larvae.

Lea suggests that the bird noted by Knowles was probably the introduced bulbul (*Molpastes fuscus*). But the record seems inconclusive, since the bird stayed on the leaf for only " over a minute " before flying off, and it is quite probable that some winged insect which it was pursuing had just settled on the leaf in question. The bulbul is very common in Suva, and on the Ra coast a nest was found in a coconut tree on which numerous larvae of *Levuana* were feeding ; but we have never seen this bird feeding on any stage of the moth, and doubt whether Knowles's conclusion (if his bird was indeed a bulbul) was correct.

The " Coconut Bird " noted by Jepson (*loc. cit.*) as being so common in Lau is probably the same bird as one known by that name in Ra which is a honey feeder and visits the flowers of coconuts.

We have received occasional reports from planters that the Mynah bird has been seen feeding on *Levuana ;* but this bird feeds mostly on the ground and does not habitually settle on coconut trees ; moreover, we have never observed it feeding on *Levuana*, so that at the most it can only be a very casual predator.

The only absolutely definite records we have of a bird feeding on *Levuana* are two instances in which fowls ate all the larvae and pupae on leaves cut from small coconut trees in a garden at Nausori and at a planter's homestead in Tailevu. In the last-named place the hens, not satisfied with the numerous larvae which they picked up from the ground, started pecking off pupae exposed by the removal of " vulu " during collecting from the base of the tree. After this, larvae were thrown one by one to the fowls, which lost no time in eating them. This is perhaps more interesting as a demonstration of the catholic taste of the domestic fowl than as a predator record of any economic value.

SPIDERS.—Several spiders nest habitually on coconut trees; but only one species, *Ascyltus pterygodes*, Koch (cf. Plate XXXIV) (ATTIDAE) feeds on *Levuana*. This is one of the commonest spiders in Fiji. Hardly a coconut tree is without a quota of individuals, and they are common on many other plants as well. This brilliantly coloured spider is one of the most valuable of all the predators on *Levuana*, because, owing to its presence at all seasons of the year on nearly every tree, it assists considerably in the final ridding of *Levuana* from those trees on which the pest has been reduced by other causes to a few individuals only.

Several unsuccessful attempts were made to ascertain the killing power of this spider by giving it *Levuana* larvae in captivity; but spiders would not feed on the larvae, and after surviving for several weeks with only an occasional house-fly as food, they died of starvation. A brood chamber of this spider, containing forty-eight newly hatched young, was collected in the field, and an attempt was made to breed the young in captivity. But this also resulted in failure because the young, which were kept in a glass jar, fed on each other rather than other food; and the few survivors died after their first ecdysis.

We therefore endeavoured to determine the predatory capacity of this spider by caging a palm loaded with *Levuana*, tanglefooting the stem to prevent the access of ants to the leaves. In this way predacious bugs and ants were screened out; but so were other insects which might form the natural food of the spider, so that the record is hardly conclusive although interesting.

During eight days one mature spider ate six out of thirteen large larvae provided; it had also apparently bitten at a pupa, but we think it very unlikely that pupae are attacked in the field.

Several instances have been noted of *Ascyltus* attacking the adult moths, in fact, small Lepidoptera seem to form its principal diet. *Levuana* is most often attacked during mating or oviposition.

Description.—The adults (Plate XXXIV) are beautifully coloured, the male with a greeny-blue sheen, the female with a dorsal yellow and black pattern. In the immature stages these bright metallic colours are not developed, the young being pale grey or straw-coloured. Powerful chelicerae are present in both sexes, and some people regard the species as likely to bite human beings; but we have never been bitten although we have handled them frequently. It is quite amusing to watch the behaviour of two or more spiders when placed in a glass jar together. They decide very quickly that there is no room for more than one of them, and they enter upon a battle royal ending in the death of all but the most powerful individual.

They construct a " retreat " on coconut trees by webbing together two adjacent leaflets—generally of one of the newly opened leaves. Within this retreat, the female eventually lays her eggs wrapt in a closely woven silk brood chamber. The young on hatching remain in the brood chamber for several days. The abandoned retreats are often used as nests by a small black ant, *Technomyrmex albipes*, Smith, var. *vitiensis*, Mann., which feeds on a mealy bug common on coconut.

The spider is diurnal in habit.

MITES.—Several different species of mites have been found associated with the eggs and pupae of *Levuana*; but with the exception of the predacious species, *Pediculoides ventricosus*, Newp., all appear to be scavengers.

Pediculoides ventricosus, Newport.—This mite was first recorded from Fiji by A. G. Carment in 1921, who found the mite preying on the pupae of *Levuana iridescens*. With the exception of Australia and New Zealand, *P. ventricosus* has been recorded from almost every country. There is quite an extensive literature on it, dealing with its attacks on grain, insects and human beings: instances of which are listed below:

SOME RECORDED HOSTS OF *P. VENTRICOSUS*.

Coleoptera	Bostrichid larvae.
	Calandra oryzae.
	Oligomerus brunneus.
	Bruchus obtectus.
	Grain pests in Argentina.
	Bruchus chinensis.
Diptera	*Meromyza americana.*
Lepidoptera	*Platyedra gossypiella.*
	Hypera variabilis.
	Cydia pomonella.
	Silkworms.
	Phthorimaea operculella.
Hymenoptera	Chalcid larvae in Coccids.
	Various parasitic Hymenoptera of grain pests.

In Fiji *P. ventricosus* has been found preying on the following insects:

Levuana iridescens.
Promecotheca reichei.
Elasmus sp. (parasitic on *P. reichei*).

Carment's record, from material collected in Suva, was the only record from Fiji until we found the mite in pupal masses of *Levuana* on the small island Toberua in February 1926. Subsequently we have taken it on *Levuana* from Navini, a small island in the Yasawa group, and Makuluva; Paine took it on Koro in December 1926, preying on the larvae and pupae and on a Chalcid parasite of the coconut leaf mining beetle (*Promecotheca reichei*). It has not, so far, been found on the cotton bollworm, a frequent host in many countries, although this insect is fairly abundant in the cotton-growing districts of Fiji.

At Navini in October 1926, we found the mite in considerable abundance amongst the cocoons of *Levuana*, and there is no question that locally it was playing an important part in control; but in view of its rare occurrence in Fiji, and the fact that, although present on Makuluva in November 1926, it was not recovered there again after twelve months, during which time there had been a continued abundance of *Levuana*, it cannot be regarded as of any great economic importance.

During the early part of 1926 we conducted breeding experiments with this mite and ascertained some interesting facts about its life-history and bionomics. But since then Herfs* has added to previous works a most comprehensive account of the mite in Germany, so that we have now little to add that has not already been put on record. But we append the following summary of our observations, since we can find no detailed account of this mite within the Australasian region.

Feeding Habits.—In only very few cases did a gravid female mite continue to feed after it had started to produce offspring. A gravid female was removed from its first food (a *Levuana* pupa) and started to produce young two days later. It was then placed on another healthy *Levuana* pupa, but as the latter was not killed the mite cannot have fed on it.

Unmated females would not live longer than four days without food. The feeding period did not exceed some two weeks, and the maximum size was in most cases attained after the first six days' feeding.

Over 200 gravid females were found on one *Levuana* pupa (cf. Fig. 76) in the field. Under such conditions very few of the mites can produce more than a few offspring, but cannibalism took place during experiments when the food supply was not renewed sufficiently frequently. Newly emerged females would attack a gravid female and feed up until they themselves fell victims to more recently produced progeny. In this way it seems possible that the species could be maintained in the field for several generations, when other food is not available.

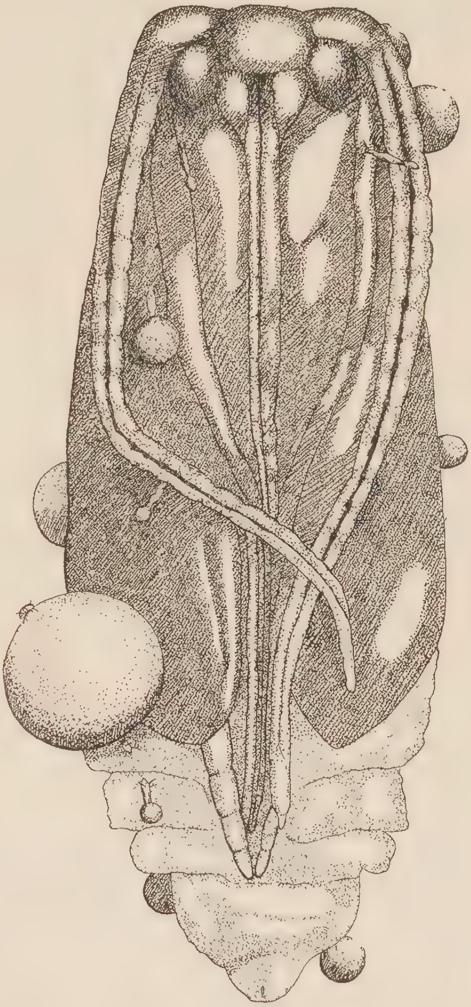

FIG. 76.—*Pediculoides ventricosus*, Newp.—Female mites feeding on *Levuana* pupa. A male mite is crawling on the body of the large gravid female on the left. × 28.

That this mite is purely predatory was proved many times by the complete failure of newly emerged females to feed on dead *Levuana* larvae or pupae which had become dried up in the slightest degree. Usually they would not survive unless provided with living food; but occasionally newly emerged females would feed on the same pupa as that to which their parent was attached, provided that it was not shrivelled.

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* A. Herfs. "Oekologische Untersuchungen an *P. ventricosus*," *Zoologica*, XXVIII, No. 74.

Mites could not feed on either larvae or pupae of *Agonoxena argaula*, the former being too active to enable the mites to gain access, the latter being too heavily chitinised to allow penetration of the fine stylets. But all stages of *Levuana* and *P. reichei* were attacked, and mites also fed in captivity on eggs of *Graeffea cocophaga*, Newp., to which they gained access by penetrating the capsule at the base of the operculum.

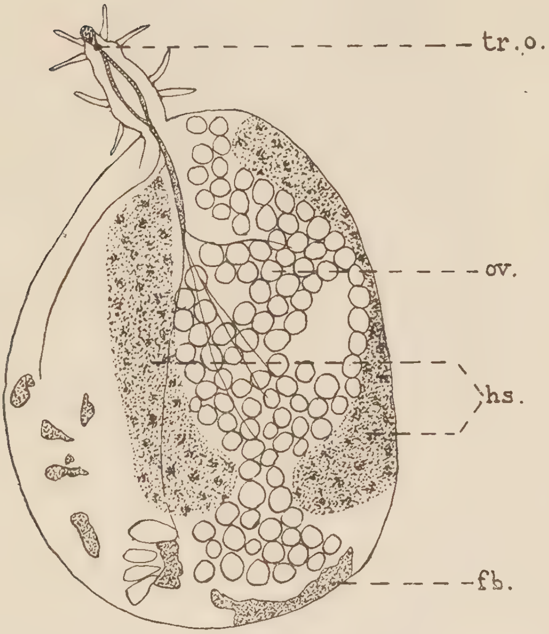

Fig. 77.—*Pediculoides.*—Lateral view of gravid female (diagrammatic). *fb.*, portion of fat body; *hs.*, hepatic sacs; *ov.*, ovary; *tr.o.*, main tracheal opening.

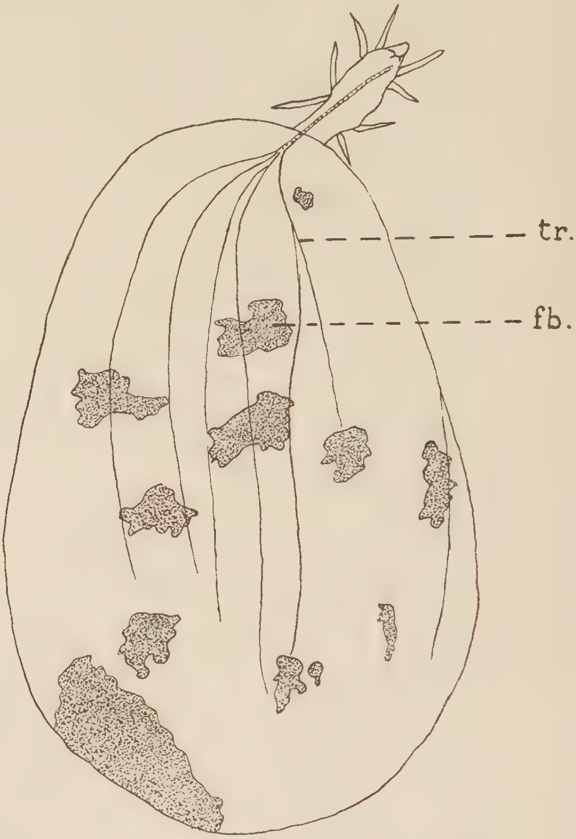

Fig. 78.—*Pediculoides.*—Dorsal view of gravid female. *fb.*, portion of fat body; *tr.*, trachea.

Some newly mated females succeeded in entering a glass tube plugged with cotton wool containing fresh pupae of *Levuana*, on which they lost no time in starting to feed.

A female with an abdomen which measured 0·38 mm. in maximum diameter was observed crawling very slowly, though movement seems to be impossible after the abdomen has swelled to more than half a millimetre in diameter (cf. Figs. 77 and 78).

The following phenomena were noted as being of interest in connection with the toxic injections made by this mite. Healthy *Levuana* pupae were used in each case as food for the mites and, since the pulsations of the dorsal vessel are readily visible, it was not a difficult matter to decide the exact time at which a pupa died.

Unmated female mites killed a pupa by merely puncturing it with their mouth parts. They did not subsequently feed on the pupa, and no blood issued from the latter where the mites had pierced it. Mites settled on a pupa just after the adult moth had started to emerge and caused its death. In these two cases it is quite evident that death to the host was caused by the injection of some toxic substance.*

The following case is interesting. A mite fed on a pupa for some twelve hours only, after which it died. Local discoloration of the host tissues took place where the mite had pierced it. The pupa, however, did not die, but continued to develop and gave rise to a perfectly normal adult moth.

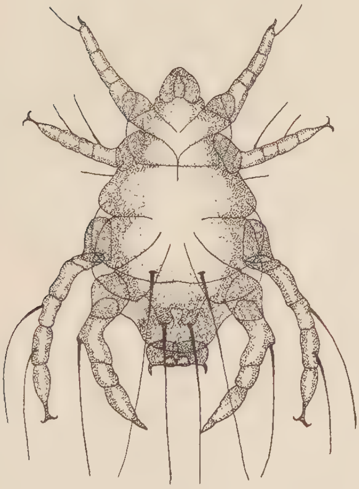

Fig. 79.—*Pediculoïdes ventricosus*, Newp. Male, × 440. Smaller setae omitted.

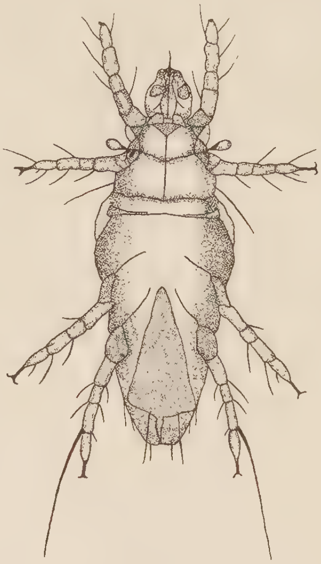

Fig. 80.—*Pediculoides ventricosus*, Newp. Female newly born. Some smaller setae omitted. × 440.

Mating Habits.—Only forty-six out of a total of 883 mites, whose birth was observed, were males (Fig. 79). This is a slightly higher percentage than that recorded by Herfs (*loc. cit.*). Females (Fig. 80) isolated after birth for twenty-four hours mated at the end of this time with a male placed amongst them, three matings occurring within the space of fifteen minutes.

Life History and Growth.—Records obtained from the breeding of thirteen fertile female mites are given in the table on p. 159. It was thought there might be a correlation between maximum size of abdomen and egg capacity, but it will be noticed that this is not so.

The death of the parent mite did not always result in the immediate death of the unborn progeny. "Nymphs" still within the uterus of the parent often continued to emerge for sometimes as long as three days after the parent female died; and no less than one male and sixteen females were, in one instance, born after the death of the parent. But seldom do all the young manage to gain access to the exterior in this way; for after dissecting a parent mite, from which young had long since ceased to emerge, a few "nymphs" and often numerous eggs could generally be found in the ovary.

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* *Vide* S. Amari, Sangyo Shikenjo Hokoku, Tokyo, III, No. 6, 1918.

We were unable to discover any six-legged phase of development within the parent uterus; so we apply the term "nymph" to denote any prenatal stage other than the ovum.

Parthenogenesis.—We made a series of experiments to ascertain whether *Pediculoides* could produce parthenogenetically,* and conclude from them that, although this phenomenon can take place, the resulting generation is arrhenotokous, and is of rare occurrence.

It is not difficult to remove with a fine bristle the newly born females from the parent body prior to mating. Eighteen were thus removed and isolated from eighteen other fertilised females. Each batch of mites was given a food supply of healthy *Levuana* pupae. The unmated females punctured and killed the pupae; but not one of them fed, and all were dead by the end of the fourth day. Of the mated ones all but four (which died) started to feed on the pupae, underwent perfectly normal growth and produced young. This result, coupled with the fact that the first mite to be born seems generally to be a male (in fifteen out of sixteen instances this was the case), thus minimising the chance of females leaving the mothersphere unmated, suggested that parthenogenesis did not occur. But, on the other hand, we found that no less than nine out of twenty-one mites, whose development was carefully observed, behaved in a manner which left little room for doubt that parthenogenesis can occur. Exactly the same feeding conditions were provided for all the mites; it was, therefore, more than a coincidence that such a large percentage of these mites produced either no offspring at all or else all males. We did not observe the initial stages in the life of these nine females, so are unable to state definitely whether or not they mated.

For the sake of comparison with the data given for fertile females in the following table, we give these data concerning the nine probably unmated females.

Maximum diameter of abdomen	0·99 mm.
Maximum feeding period	15 days.
Maximum length of life	34 ,,
Minimum age at first birth	12 ,,
Maximum young from one parent	2 males.

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* Herfs records that unmated females do sometimes leave the mother sphere and reproduce parthenogenetically, their offspring being all males.

No. of parent mite	1	2	3	4	5	6	7	8	9	10	11	12	13
Max. diameter of abdomen (in mm.)	0·79	0·72	0·99	0·93	0·86	0·61	0·94	0·89	**1·22**	0·71	0·76	1·1	1·12
Feeding period (in days)	7	6	11	8	7	8	9	8	**12**	[7]	[8]	[6]	[6]
Length of life (days)	20	25	15	13	16	13	16	26+	13+	**29**	21	11	12+
Age of parent at time of first birth (days)	8	7	9	10	8	8	10	9	8	8	9	8	**6**
Period during which young were born (days)	13	17	8	6	8	7	7	17+	5+	**21**	14	6	6+
Maximum number of young produced in twenty-four hours	2 ♂ 17 ♀	— 12 ♀	— —	— 10 ♀	1 ♂ 8 ♀	— 9 ♀	— —	— 16 ♀	**1 ♂** **28 ♀**	— 11 ♀	— 12 ♀	1 ♂ 9 ♀	1 ♂ 9 ♀
Total number of young born	7 ♂ 119 ♀	5 ♂ 81 ♀	2 ♂ 62 ♀	3 ♂ 52 ♀	4 ♂ 20 ♀	2 ♂ 31 ♀	3 ♂ 29 ♀	4 ♂ 139 ♀	4 ♂ 61 ♀	3 ♂ 89 ♀	4 ♂ 85 ♀	3 ♂ 35 ♀	2 ♂ 27 ♀
Number of young born after death of parent	1 ♂ 9 ♀	none ,,	— 8 ♀	— 7 ♀	none ,,	— 6 ♀	— —	— —	— —	none ,,	— 3 ♀	**1 ♂** **16 ♀**	— —
Number of unborn progeny found on dissecting parent mite	69	0	4	4	11	2	2	13	37	1	0	6	8
Total egg capacity	132	86	68	59	35	35	34	**156**	102	93	89	44	37

DATA CONCERNING THE LIFE HISTORY, ETC., OF *PEDICULOIDES VENTRICOSUS*, NEWP.

Thirteen female mites fed on healthy *Levuana* pupae, which gave birth to male and female progeny.
Nos. 1–7 were left on their host until they died.
Nos. 8, 9 were killed before all the young were born.
Nos. 10, 11 were removed from their host on the seventh and eighth day respectively.
No. 12 was removed from its host the day after it first gave birth.
No. 13 was removed from its host the day after it first gave birth, but was killed prior to completion of parturition.
Means of temperature during the experiment were maximum 85°, minimum 78°.
[Maxima and minima of interest are in black figures.]

Ants.—Four different species of ants have been observed attacking the immature stages of *Levuana,* and there seems little doubt that under certain conditions these insects play an important part in eradicating the moth from those trees on which they have nested.

The small number of observed cases of ants attacking the moth seems quite incompatible with such a frequently occurring and extensive *Levuana* mortality, inexplicable unless due to predatory attacks by ants. Ants are not easy insects to study by field experiments because their habits are variable and they tend to produce most effect on trees in which they have nested. Most of the experiments designed to ascertain ant control proved inconclusive, and the data we have obtained concerning their activities resulted from experiments designed for other purposes.

The inclusion of two species, *Paratrechina* (*Nylanderia*) *vividula* and *Pheidole megacephala,* in the list of predators is based in each case on a single field observation, so that no conclusions can be drawn regarding their utility.

Tapinoma melanocephalum, F.—The first time that this ant was observed attacking *Levuana* was at Nasese in May 1926, where young larvae on hatching from the egg were seized by ants and carried off to their nest constructed in the basal angle of a leaflet. In this instance the attacks of the ant were most persistent, and only 150 larvae could be found on a leaf on which no less than 536 eggs had been pinned a week previously. Ants were seen waiting about on the leaflets on which egg-masses had been pinned ; and as soon as a larva hatched, it would be seized and carried away by an ant. The latter never attempted to attack unhatched eggs, and as the mortality amongst the surviving larvae decreased progressively during subsequent development, the attacks of the ant seemed to be limited to the smaller larvae.

This ant, which has a wide distribution in the tropics, is one of the commonest in Fiji. It seems to thrive under dry conditions and is very common in houses. It has been called the " small crazy ant," and its peculiar jerky method of crawling certainly warrants the application of the name.

It is a very pale-coloured species, except for the dark head, and being of small size is not very conspicuous. The nests are constructed in any sheltered part of a tree, generally amongst the " vulu." In the dry zone of Vitilevu it is one of the commonest ants nesting on coconuts, and there it seems to act largely as a scavenger, often removing all traces of old *Levuana* pupal masses. Like other members of the genus, it has, when crushed, a characteristic odour resembling rancid butter. We do not know when it was first introduced into Fiji.

Since this predatory ant is extremely abundant in the dry zone of Vitilevu, it is possibly a controlling agent of some importance in that area.

Tetramorium guineense, F.—This ant occurs very widely in the wet zone on coconut trees, but it was not taken on the other side of the island.

It is recorded as a house ant in Mississippi and as a predator on the Paddy borer in Formosa. It also occurs in British Guiana, the Solomon Islands and

Malay, and will probably have by now found its way all over the Southern Pacific.

It is a medium-sized, reddish-brown ant with powerful mandibles, and it attacks both the larvae and pupae of *Levuana*, reaching the latter by breaking open the cocoons. It became established on the small palm growing inside our large wire breeding cage and was the cause of the sudden heavy mortality that occurred amongst the larvae and pupae of the fourth generation bred inside the cage. Since then all attempts to breed the moth inside the cage have been spoilt by the wholesale destruction of the early stages by this ant. In October 1927 only one individual reached maturity out of 1,700 eggs pinned on the caged tree ; whereas on an adjacent tree outside the cage not infested with *T. guineense*, 34 per cent. of the eggs pinned on reached maturity in spite of exposure to parasitism by *Ptychomyia* and to those predators that could not gain entry to the cage.

Proof that this ant was alone responsible for the destruction of immature *Levuana* on the caged palms was obtained by an experiment conducted in November 1927.

Levuana eggs, to the number of 500, were pinned on to each of two leaves of the caged palm. One leaf, (*a*), was trimmed so as not to touch other leaves or the walls of the cage, and was rendered ant-proof by a thin band of tanglefoot round the petiole not wide enough to prevent the spider *A. pterygodes* —present in the cage—from jumping on to the leaf. The other leaf, (*b*), was left untouched. In addition to this, a similar number of eggs were pinned on to a leaf, (*c*), of a tree just outside the cage, this leaf being left untouched as in the case of (*b*). Twelve days after the eggs were pinned on to the leaves, a count was made of the larvae feeding on the three leaves.

On leaf (*a*) all the egg-masses hatched and numerous larvae were feeding. No signs of any extensive work in spite of the fact that a female *Ascyltus* with several young were on the leaf.

On leaf (*b*) all the egg-masses had hatched, but only a few feeding scars of first-stage larvae were found, and not a single larva could be found on the leaf.

On leaf (*c*) all the egg-masses had hatched and 95 per cent. of the larvae were found feeding on the leaf. The only ants found on this tree were *P. megacephala* and *Technomyrmex albipes* var. *vitiensis*, neither of which can have attacked the larvae to any great extent.

No further losses were incurred on leaf (*a*) and only a few on leaf (*c*), so that the evidence for the predatory nature of *T. guineense* was very convincing.

Unfortunately, however, this ant does not seem to establish itself on many trees, and it is quite possible that its voracity as a predator on *Levuana* was, in the above described instance, enhanced by some special conditions provided by the caging of the palm.

Pheidole megacephala, F.—This ant, now the commonest house ant in Suva, was first recorded from Fiji in 1919 by Veitch. It is cosmopolitan in distribution and has been variously spoken of as beneficial and harmful.

It is not one of the commonest ants on coconut trees, but has a very wide distribution in the field. The only occasion on which it was recorded as attacking *Levuana* was on the Ra coast in June 1925, when it carried away to its nest some almost mature *Levuana* larvae. But its presence on leaf (*c*) of our *Tetramorium* experiments (see above), where so few larva were destroyed, is evidence that *Levuana* is not one of its staple foods.

Paratrechina (*Nylanderia*) *vividula*, Nyl.—This medium-sized black ant was seen carrying away unhatched eggs of *Levuana* on a small tree at Laucala (Rewa) in November 1925. The ant was not particularly abundant on the tree and only a few specimens were procured. This was the only occasion on which this ant was encountered during our investigations of the moth. It has obviously not been an important predator.

Polistes macaënsis, F.—It is doubtful whether this insect, the common Fiji hornet, ever attacks *Levuana.*

Knowles (*loc. cit.*) said of it : " There appears to be a strong impression that the so-called hornet (*Polistes hebraeus*), which is exceedingly common in this part of the island (the dry zone of Vitilevu), plays a part in reducing the numbers of *Levuana.*"

We have never seen an instance of hornets attacking *Levuana ;* but they do attack many caterpillars and, moreover, frequently visit coconut trees, if for no other purpose than to collect the " down " off newly opened leaves for constructing their nests, so that it seems probable that on occasions they may attack *Levuana.* This species is certainly not the sole cause in reducing *Levuana* in the dry zone.

PREDACIOUS BUGS.—Four species of PENTATOMIDAE have been recorded by various observers as predacious on *Levuana iridescens.* Three of these species (*vide* Plate XXXIII)—*Cantheconidea cyanacantha*, Stål ; *Platynopus melanacanthus*, Boisd. ; *Oechalia consocialis*, Boisd.—are, so far as we have observed, entirely predacious. The fourth, *Tectocoris lineola*, F., is well known as a cotton pest, and although on two occasions it has quite definitely been recorded as attacking larvae of *L. iridescens*, we do not consider that it was ever more than an extremely occasional predator.

Tectocoris lineola, F.—In 1906 Knowles (*loc. cit.*) observed a larva of " a large blue Pentatomid bug " attacking the larvae of *Levuana* in the field. He remarks that it killed two more in captivity. The only other record of the predacious activity of this bug was made by Veitch at Nandi in 1916, where he found it attacking larvae of *Levuana* on a small coconut tree on a plantation. The insect is too well known to require any description here.

The other three predacious Pentatomids were each more important than *T. lineola* from the point of view of *Levuana* control. All three species were common and widely distributed in the *Levuana* areas until the middle of 1926, and during outbreaks one or more species would become very abundant locally ; but in spite of this we cannot share the view of Jepson (*loc. cit.*), who considered that *Levuana* outbreaks were actually controlled by the ravages of the bug *C. cyanacantha.* There is no doubt whatever that when *Levuana* had been reduced in numbers by other causes until only a comparatively few individuals remained on certain trees, the bugs together with spiders assisted greatly in ridding such trees of the remaining larvae, and in such a way preventing a recurrence of attack on those trees until they became reinfested by a flight of the moth from elsewhere.

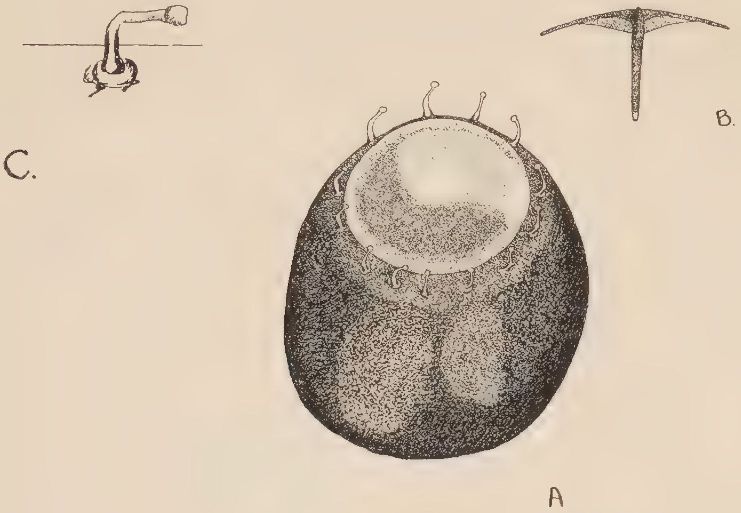

FIG. 81.—*Cantheconidea cyanacantha*, St.—A. Egg, × 80. B. Hatching denticle, × 84. C. Chorionic process, × 106.

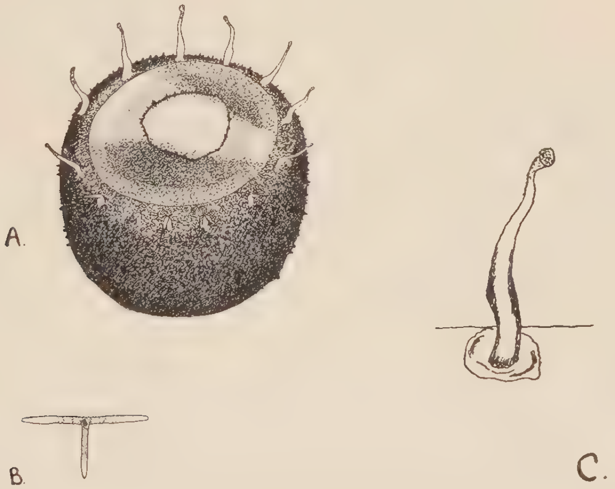

FIG. 82.—*Oechalia consocialis*, Boisd.—A. Egg, × 80. B. Hatching denticle, × 84. C. Chorionic process, × 106.

We have never seen a single individual of any one of these three bugs feeding on *Levuana* since July 1926, although we have made frequent visits to the few remaining localities where the moth is still to be found. The bugs, more particularly *C. cyanacantha*, which is indigenous, probably all have a wide range of hosts, and they must have been attracted by the relatively abundant food supply offered by an outbreak of *Levuana*, where with the scarcity of other natural enemies of the moth their importance became exaggerated. Quite apart from the fact that the eggs of all three species are heavily parasitised, which checks their powers of increasing rapidly, their capacity for destroying larvae of *Levuana* in captivity experiments was not great enough to warrant including them amongst the primary agents which caused the cleaning up of outbreaks prior to 1925.

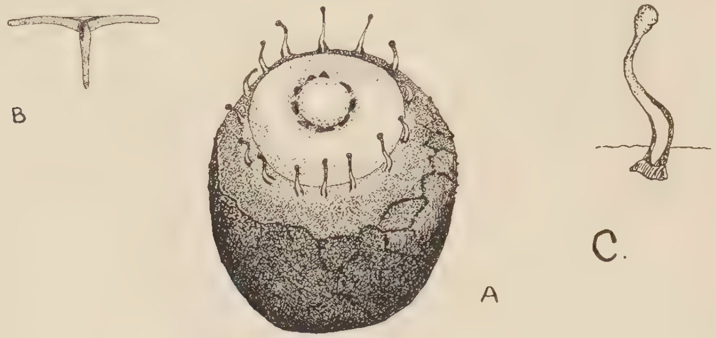

Fig. 83.—*Platynopus melanacanthus*, Boisd.—A. Egg, × 80. B. Hatching denticle, × 84. C. Chorionic process, × 106.

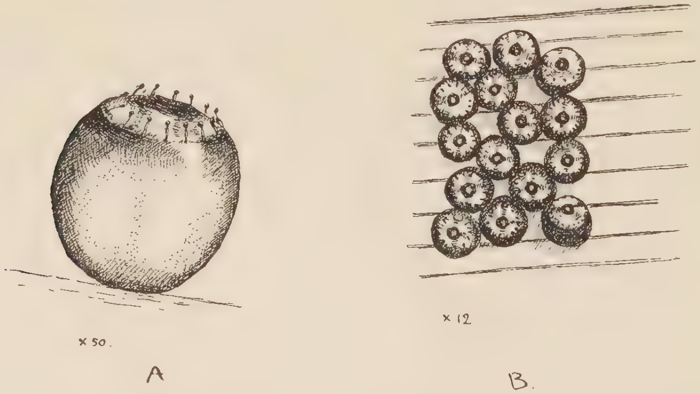

Fig. 84 —*Platynopus melanacanthus*, St.—A. Side view of egg, × 50. B. Egg-mass on part of coconut leaf viewed from above, × 12.

The following key for determination of these predacious Pentatomids was primarily designed for field use at a time when all three species were likely to be found together; it incorporates the most distinctive characters of the three species.

KEY FOR DETERMINATION OF THREE PENTATOMIDS PREDACIOUS ON L. IRIDESCENS.

Eggs. (Figs. 81, 82, 83, and 84.)

1. Chorionic processes as long as half the diameter of the operculum, swollen at the tip, and for the basal third of the length. Eggs—black	*O. consocialis.*
2. Chorionic processes less than one-third of the diameter of the operculum; swollen at the tip, but greatest width at the base. Eggs—bronze or brown	3
3. Chorion of egg smooth; operculum with central hyaline spot. No central ring of opercular spines; chorionic processes extremely short and rather widely spaced round the egg	*C. cyanacantha.*
4. Chorion of egg covered with short, dark, irregularly spaced lines often connected by ridges forming a lattice-like ornamentation; operculum with a central circlet of similar spines, and without central hyaline spot. Chorionic processes larger, not so widely spaced	*P. melanacanthus.*

Nymphs.[*] (See Plate XXVI.)

1. Middle and hind tibiae with a complete median band of white	*C. cyanacantha.*
2. Tibiae without such a band	3
3. Small spur on central face of front femur	*P. melanacanthus.*
4. Front femur lacking a spur	*O. consocialis.*

Adults.

1. Scutellum terminating posteriorly in a point	*O. consocialis.*
2. Scutellum rounded posteriorly	3
3. Tip of scutellum luteous, suffused with dark-brown punctures. Lateral angle of scutum not very prominent and ending in a single blunt point	*C. cyanacantha.*
4. Tip of scutellum pale yellow (flavous), not suffused with brown. Lateral angles of scutum very prominent and ending in a sharp double point	*P. melanacanthus.*

Cantheconidea (*Canthecona*) *cyanacantha*, Stål

1. *History and Distribution.*—This bug was described from the Fiji Islands by Stål in 1870,[†] since when there have been several further records of it from Fiji, but none from any other country so far as we can discover. Knowles (*loc. cit.*) took it in 1906 feeding on a caterpillar on *Hibiscus*, but Jepson, in 1916, was the first to observe its attacks on *Levuana iridescens* and to claim it as an important predator.

During the season 1925–26, when we were making a fairly constant survey of the main *Levuana* outbreaks, *C. cyanacantha* was not so abundant as either *O. consocialis* and *P. melanacanthus*, but we have on two occasions (Namosi and Upper Waimanu) taken it in the native bush some distance from the nearest *Levuana*-infested locality.

2. *Hosts.*—With the exception of Knowles' record in 1906 we know of

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[*] This key applies to the last three instars only; it is not possible to distinguish the nymphs of the first two instars by means of a key. They are all red and black in colour and too small for field determination.

[†] *Svenks. Vet. Akad. Handl.*, ix, p. 42, 1870.

no absolutely definite records of this bug attacking insects other than *Levuana*, although there is no doubt that it must feed on several other insects. Apart from the instances quoted above of finding it in the bush, we have seen nymphs at Lami on *Solanum torvum* on which the only other insects were larvae and adults of a plant-feeding Coccinellid (*Epilachna cardinalis*). None of the bugs were actually seen feeding on the beetles. On another occasion, nymphs were seen on a common "rain" tree—*Albizzia lebbek*—and were almost certainly feeding on the larvae of *Eublemma*, on which they were subsequently reared in captivity. We tried, without success, to feed the bugs on larvae of *Agonoxena argaula* in captivity. With *Levuana*, they showed no particular preference either for parasitised or healthy larvae, although even when starved for three days they refused to feed on the puparia of *Ptychomyia remota*.

3. *Life-history*.—Jepson bred the bugs in captivity, worked out their life-history and ascertained their killing power on *Levuana*. He only mentions four larval instars, and he possibly overlooked the first moult before which the nymphs do not feed. We propose, therefore, to give further details of the early stages, which we worked out in Suva in the winter months of 1925.

The life cycle of this bug was worked out with specimens kept in captivity and fed on *Levuana iridescens* larvae.

Incubation period	9 to 10 days.
First instar nymph	4 ,, 6 ,,
Second instar nymph	4 ,, 5 ,,
Third instar nymph	4 ,, 5 ,,
Fourth instar nymph	4 days.
Fifth instar nymph	7 ,,
Total duration of immature stages . .	Max. 37 days, min. 32 days.
Emergence of adult to first oviposition .	10 days.
Total life cycle	6 to 7 weeks.

The adults probably live for a considerable time ; we fed one female in a small glass jar in the laboratory for ten weeks, during which time it laid a total of 288 eggs.

Jepson records a total immature period of twenty-five days. He made his experiments in September to October 1916, whereas ours were made in June and July. As there was a plentiful food supply provided in both instances, we must suppose that the development of this bug is accelerated by warmth, the average temperature for October being a few degrees higher than that for June and July.

4. *Habits*.—Except during the first instar after hatching from the egg, nymphs and adults of *C. cyanacantha* subsist normally on a predacious diet.

Their methods of feeding are probably typical for any species of predatory bug and need no special description, but we think that the juices injected into the prey, possibly to facilitate a certain degree of external digestion, have a decided toxic effect on the host, a matter that will be discussed further in a later section.

The bugs are diurnal in their habits, although they are attracted to a light at night.

The eggs are laid in clusters on any part of the plant on which the host is feeding. The number of eggs in each cluster varies from eleven to thirty-four and is seldom fourteen (cf. *O. consocialis*). The newly hatched nymphs remain huddled together in a mass, generally selecting some sheltered place in which to pass through their inactive first-instar period. We discovered, after several abortive attempts to breed the nymphs in captivity, that during the first instar their only requirement is moisture in an easily accessible form. In nature they get all they require from the dew or other surface moisture on a leaf; but in captivity we were unable to rear them unless water, either on a moistened plug of cotton wool or else smeared over a piece of leaf, was placed in the breeding jars.

After the first moult, the nymphs begin their predatory habits. Even second instar nymphs are " game " to tackle a mature *Levuana* larva, and they would frequently be dragged along by their prey as they fed. But the bug would sooner or later weaken the larva so much that the latter would cease its movements and gradually die.

Nymphs and adults of this bug are cannibals when other food is not available, a newly moulted nymph at such times is readily preyed upon by its congeners, and the eggs are often eaten by half-starved adults.

Mating is repeated several times during the egg-laying period; when a female is isolated, she will start to lay infertile eggs after about six weeks, the supply of spermatozoa being then apparently exhausted.

Normally the percentage of infertile eggs is very low (less than 1 per cent.), based on collections of eggs from the field, although there is a tendency for the bug embryos to die when just ready to hatch, and this causes about a 5 per cent. mortality in each brood. We could find no obvious cause for this prenatal death of fertile eggs.

The egg capacity of these bugs seems to be in the neighbourhood of 300, 288 eggs being obtained from one female kept entirely in captivity.

5. *Usefulness as a Predator.*—Jepson (*loc. cit.*) fed *C. cyanacantha* in captivity on larvae of *Levuana* and made some valuable observations on their killing powers. He found that adult bugs each consumed mature *Levuana* larvae at the rate of 13·5 per diem; and that a bug during its immature stages consumed seventy-six larvae, an average of four larvae per day.

On two occasions we made feeding tests with isolated female adult bugs, and over a period of two weeks obtained an average daily consumption of 3·5 and 7 mature host larvae respectively. But during the period concerned neither of the female bugs laid any eggs, and that may account for their lack of appetite.

The most interesting thing to us was the rapidity with which a host larva would become comatose after being attacked by the bug. We tested this experimentally by allowing an adult female bug to pierce six fully grown *Levuana* larvae with its proboscis, after which the larvae were immediately removed from it. Not a single larva managed to survive the effects of the attack, although they were removed from the bug long before this latter had time to deprive them of any appreciable quantity of body fluid. We therefore conclude that adult bugs (and possibly the nymphs as well, although the effect is then not so clearly marked) inject a toxic substance into the body of their prey, which eventually causes the death of the latter.

As we have remarked above, we think that Jepson attached undue importance to this bug as a controlling factor on *Levuana*. While still maintaining our opinion in this matter, we believe that the species must have been much commoner in Jepson's time than it was in 1925 during our study of the *Levuana* position prior to the introduction of *Ptychomyia*. The other predatory Pentatomids, *O. consocialis* and *P. melanacanthus*, were more plentiful than *Cantheconidea* in the *Levuana* districts during 1925–1926, and we are of the opinion that *O. consocialis* at least is a recent arrival in Fiji and that it has increased rapidly on *Levuana* at the expense of *C. cyanacantha*. We will discuss the evidence to support this view under the heading of the species concerned.

6. *Natural Enemies.*—The eggs are attacked by *Microphanurus giraulti*, and probably also by a species of *Telenomus*, although we have no certain record of the latter species breeding through.

We have seen no other natural enemies of the bug in Fiji. The two egg-parasites also attack the eggs of the other two predatory bugs, and a general account of them will be found elsewhere.

Platynopus melanacanthus, Boisduval

Pentatoma melanacanthum, Boisd., 1835 *

1. *Historical.*—This insect was described by Boisduval in 1835 from Dutch New Guinea. Kirkaldy (*op. cit.*) lists it from Moluccas, Papua, New Caledonia, Ligu and Murua, as well as Fiji (Vitilevu), from where he examined specimens taken by Muir at Rewa in 1906. It is not known whether this bug is a comparatively recent introduction to Fiji, but we incline to that view since its eggs might quite possibly have been carried from one of the island groups to the westward during the nineteenth century when labour was being recruited to Fiji.

As far as its attacks on *Levuana* are concerned, it seems remarkable that Jepson did not come across it during his extensive work here. We do not know whether Muir's specimens were feeding on *Levuana*. Lea took it in Taveuni in 1924 outside the *Levuana* region. The first definite record of this species attacking *Levuana* was made in June 1925, when material was collected from estates on the Ra coast of Vitilevu. Since then, it has been taken at various localities on Vitilevu, on Beqa and Ovalau (ii/26) ; and H. Maréchal took it again on Taveuni in 1927.

2. *Hosts.*—We have no records of any hosts other than *Levuana* for this bug, although it is obvious from its distribution in Fiji that such must exist.

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* "A Catalogue of the Hemiptera of Fiji," *Proc. Linn. Soc.* N.S.W., 1908, vol. xxxiii, Pt. 2, G. W. Kirkaldy.

3. *Life-history.*—This was worked out in January 1926 with specimens fed on *Levuana* larvae in Suva.

Incubation period	5·0 to 7 days.
First instar nymph	2·5 ,, 3 ,,
Second instar nymph	2·5 days.
Third instar nymph	2·5 ,,
Fourth instar nymph	3·0 ,,
Fifth instar nymph	4·0 ,,
Total duration of immature stages	19·5 to 22 days.

Emergence of adult to oviposition was eighteen days (only one instance).

Total life cycle, 5½ weeks.

We kept a female alive in the insectary for seven weeks.

The comparatively short period taken for the developmental stages of this bug in January is interesting when compared with that of *C. cyanacantha* in July. It bears out our statement that temperature has probably a decided influence on the rate of development.

4. *Habits.*—The feeding, mating and egg-laying habits of this insect are like those of *C. cyanacantha*, and it would involve useless repetition if we wrote a separate description of them here; so that, unless otherwise stated, what we have said about the habits of the latter insect is applicable also to *Platynopus*. It was found that a nymph took just two hours to exhaust completely the food supply in one full-grown *Levuana* larva.

Infertile eggs, and eggs in which the embryo dies just before hatching, occur with *Platynopus* in much the same proportions as with *Canthecona*.

The egg capacity seems to be about 300, as in *Canthecona*. A female laid 299 eggs during her life in captivity, and four more unlaid eggs were found in the oviduct and ovaries after death, making a total capacity of 303 eggs for one female.

5. *Usefulness as a Predator.*—We made the following observations on the killing power of this bug by feeding it on *Levuana* larvae in captivity. One adult female bug killed 176 larvae in ten days, an average of 17·6 larvae per diem. Many of the larvae used for food were not full grown, and on one day the bug killed no less than thirty larvae. On the other hand, a newly emerged male and female bug during four days accounted for only fifty-six full-grown larvae, an average of seven each per diem.

During the predatory phase of the immature stages (*i.e.* second, third, fourth and fifth stage nymphs), a bug nymph killed sixty *Levuana* larvae during the twelve days it took to become mature, an average of five per diem.

Platynopus was fairly abundant in *Levuana* outbreaks in 1925–26, but was probably not so common as *Oechalia*. While helping to maintain the scarcity of *Levuana* in non-outbreak localities, it had little controlling effect on the brood of the moth when once the latter had become numerous.

6. *Natural Enemies.*—The only natural enemies observed in Fiji were the two egg parasites, *M. giraulti* and *Telenomus* sp., an account of which is given elsewhere (p. 172).

Oechalia consocialis, Boisduval

1. *History and Distribution.*—During the latter part of 1924, Mr. Simmonds, the then acting Government Entomologist in Fiji, proposed the introduction to Fiji from Australia of the predacious Pentatomid, *Oechalia shellembergi*. It was agreed that the introduction of this bug as a predator on *Levuana* was desirable, and the local Government asked an entomologist in New South Wales to try to procure a shipment of the bug for Fiji. Apparently the bug was at that time unprocurable, and the project was abandoned for the time being.

During June 1925, Paine took a Pentatomid feeding on *Levuana* at Nanuku plantation on the Ra coast of Vitilevu. He mistook this bug at the time for *Cantheconidea cyanacantha*—hitherto the only Pentatomid recorded as preying on *Levuana*. The British Museum determined specimens of this bug as *Oechalia consocialis*—a new record for Fiji.

Simmonds went to Tahiti in 1920 to collect parasites of *Aspidiotus destructor* for introduction to Fiji. He saw there the bug *O. consocialis*. Although no express efforts were made to introduce this bug at the time, we are inclined to the view that it was accidentally introduced on some small coconut palms sent by Mr. Simmonds from Tahiti to Fiji. Apparently these palms were actually planted in Suva, and if an egg-mass of the bugs happened to be on one of them, the nymphs would not have had to crawl far to find an abundant food supply in *Levuana iridescens*, and these would rapidly have established the species in Fiji.

In view of the facts that this bug was the most abundant of the bug predators on *Levuana* during 1925, that we only found it on Vitilevu and Ovalau and never in the bush, and that it had not been seen in Fiji before, it seems probable that it was introduced from Tahiti in 1920.

It has been recorded from Australia, New Zealand, the Marquesas and Tahiti.

During 1925–26, we took it on Vitilevu at Nanuku, Caboni and Lami ; also on Nukulau, Ovalau and Moturiki.

2. *Hosts.*—In Fiji we have never seen or heard of this bug attacking any insect other than *L. iridescens*.

In Australia it has been recorded as predacious on the larvae of the vine moth, *Phalaenides glycine*, several cutworms, and larvae of the fig leaf beetle, *Galeruca semipullata*.

3. *Life-history*.

Incubation period	3 * to 6½ days.
First instar nymph	1·75 to 2 days.
Second instar nymph	2 days.
Third instar nymph	1·75 days.
Fourth instar nymph	2·5 days.
Fifth instar nymph	4 days.
Total duration of immature stages . .	15 to 19 days.
Emergence of adult to first oviposition was	4 to 12 ,,
Total life cycle	3 to 4 weeks.

Mating took place two days after emergence.

Adult female lived in captivity for eight weeks.

* January 1926.

This is the shortest life cycle of any of the three Pentatomids under consideration. Some of the records were made during January and February, but these months were not exceptionally warm in 1926, and we think that a life cycle of two and a half weeks is probably the average for this bug in Fiji at all seasons.

4. *Habits.*—Most of the habits of this bug are entirely similar to those of *C. cyanacantha* and *P. melanacanthus.* We will only mention here the points in which it differs.

More than half of the fifty egg-masses examined contained either fourteen or twenty-eight eggs in each mass. The highest number recorded in one batch was forty-five and the lowest four. It is interesting that a plant-feeding Pentatomid (*Axiagastus campbelli*, Dist.) in the Solomons also lays usually fourteen eggs in each mass.

Three females laid 652 eggs in captivity; as one of them died after laying 50 eggs, the egg capacity of the species would appear to be about 300 as in the other bugs just described.

Infertile eggs and failures of fully formed embryos to hatch occur in the same proportion with this as with the other bugs.

5. *Usefulness as a Predator on Levuana.*—An adult female bug killed 132 *Levuana* larvae (mostly fully grown) during the course of ten days' feeding, an average killing power of 13·2 per diem. A male and female kept together disposed of fifty-six larvae in seven days, an average of only four larvae each per diem. On two occasions during the latter experiment the bugs finished the entire food supply provided, so that the figures are probably on the low side.

We were under the impression that *Cantheconidea cyanacantha* was a valuable predator on *Levuana*, and having found *O. consocialis* in the field and mistaking it at that time for *C. cyanacantha*, we decided to breed up a stock of the bug in captivity and liberate colonies in the worst *Levuana* outbreaks, where the bug had not been seen. With this end in view we left a small number of bugs (reared from eggs taken at Nanuku, v/25) in a large breeding cage containing a small palm on which numerous *Levuana* larvae were loaded. The bugs bred rapidly in the cage as long as the supply of food was maintained, and we liberated colonies on Naigani and near Lautoka.

This bug, although subject to the attacks of two egg parasites, succeeded in becoming very plentiful and widely distributed towards the end of a *Levuana* outbreak. At Caboni, ix/25, not a single tree examined was without traces of its egg-masses, many of which were heavily parasitised. And yet, in spite of its abundance in this locality, the bug was unable to prevent *Levuana* from increasing on that estate until the complete food shortage condition was reached. So that although more abundant than the other two bugs, we think that, like them, its only real use as a predator was during the times when *Levuana* was greatly reduced in numbers.

6. *Natural Enemies in Fiji.*—The eggs are attacked by the two egg parasites *Telenomus* sp. and *Microphanurus giraulti.* Apart from them, no other agents of natural control have been observed.

EGG PARASITES OF PREDACIOUS BUGS.—We have bred two species of parasites from the eggs of the three bugs which attack *Levuana* (*T. lineola* excluded). One of these species was very abundant in the Ra coast plantations where it was first observed. Subsequently the same species was obtained in Lomaiviti. The other species was only taken once by us on Beqa. McNamara in 1924 reported that the eggs of the *Levuana* predacious bugs were " heavily parasitised " on Ovalau. We are unable to say what parasite species he referred to, as we never saw any specimens bred out by him. We have examined a slide of a male and female parasite made by Simmonds labelled " Suva 24–5–24, from ova of Pentatomid," and can see no difference between this and the species we subsequently bred out on Beqa. Unfortunately, we do not know from which species of Pentatomid Simmonds's parasites were bred, but it was one of the three predacious forms referred to above. We are provisionally regarding Simmonds's material as *Microphanurus giraulti*.

EGG PARASITES OF PREDATORY PENTATOMIDS.—1. *Microphanurus giraulti*, Dodd.—This Proctotrupid parasite was bred from eggs of *P. melanacanthus* collected at Beqa in February 1926. Prior to that Simmonds bred out the same, or a nearly allied species, in Suva. We have only this one record of its occurrence, never having bred it from any eggs since. With the parasites bred out in Suva from the Beqa egg-mass we were able to determine the duration of the life cycle and try the parasite with eggs of *O. consocialis* and *C. cyanacantha*, both of which species it readily attacked.

The total life cycle varied from 13 to 15 days :

ex *C. cyanacantha*	14 days.
	15 ,,
ex *P. melanacanthus*	14 ,,
	14 ,,
ex *O. consocialis*	13 ,,
	14 ,,
	15 ,,

Host eggs dissected seven days after they were stung by the parasite contained pupae, so that the egg and larval stages of the parasite must be less than a week, and the pupal period at least seven days. A female was kept alive for twenty-five days in captivity ; a male for twenty-one days.

Habits.—Oviposition takes two to five minutes, being most rapid when a female first commences to lay. The ovipositor is usually inserted into the egg of the host below the ring of chorionic processes. One female under observation stung twenty-seven bug eggs during the space of an hour, and twelve more during the next three-quarters of an hour with a total of thirty-nine in $1\frac{3}{4}$ hours.

We allowed a female parasite to sting eggs which had been stung by the other egg parasite (*Telenomus*) twelve days previously. Although *M. giraulti* appeared to lay in four of the eggs, we obtained adults of *Telenomus* from each of those eggs two days later, so that it is improbable that *M. giraulti* is hyperparasitic on *Telenomus*.

The parasites usually attack host eggs not more than four days after they were laid. A parasite stung a bug egg which contained an embryo bug almost ready to hatch, but no parasite bred out, although the bug embryo was killed.

We attempted to determine the egg capacity of *M. giraulti* and got a record of 100 eggs actually laid. Eighty of these produced adult progeny, most of the remainder dying as mature pupae inside the host egg and a few being infertile.

This parasite is very similar in general appearance to the other commoner bug egg parasite *Telenomus* sp. We could find no character by which they could be distinguished in the field, and eggs of the host parasitised by either species have a similar appearance (see Fig. 85).

When examined under a microscope, they can be distinguished at once by the length and spacing of the antennal joints and the shape of the tarsal joints.

2. *Telenomus* sp.—In June 1925 Paine bred a small black parasite from eggs of *O. consocialis* at Nanuku (Vitilevu). This was determined at the British Museum as a species of *Telenomus.* No further specimens were obtained at the time, but during a second visit to the same locality in September, a *Levuana* outbreak had almost finished over a wide area, and egg-masses of the three common predacious bugs were found on nearly every tree examined, *O. consocialis* being the most abundant. A large number of egg-masses were parasitised—probably mostly or wholly by the *Telenomus* —the only species actually seen there. On one tree ten out of fourteen bug egg-masses were parasitised. A *Cantheconidea* adult female was seen with four adult egg parasites on her back, which were no doubt waiting for her to oviposit.

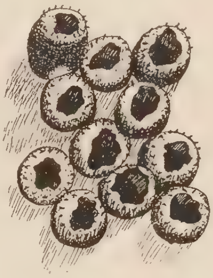

FIG. 85.—Batch of eggs of *P. melanacanthus*, Boisd., showing emergence holes of parasite *Microphanurus giraulti*, Dodd.

It is interesting that, although the egg parasitism was not high enough to check a fairly rapid increase of the bugs, yet the latter failed to control *Levuana*, which had been active on the estate for nearly two years. By the end of this time, the trees were completely defoliated over almost the entire estate. Defoliation, coupled with the typical high mortality from massing of pupae, was almost certainly the cause of the rapid reduction in numbers of the moth.

A female parasite bred from an egg-mass of *O. consocialis* taken on Moturiki in March 1926 was indistinguishable from the *Telenomus* seen at Ra. Pending determination by the British Museum, we are considering the two forms as the same species.

The following notes on the life-history and habits of this parasite were all obtained from the progeny of the Moturiki female.

Life-history.—Fifteen days from oviposition to adult emergence, *ex* eggs of *P. melanacanthus.*

Hosts.—*O. consocialis*, *P. melanacanthus* and probably *C. cyanacantha.*

Unfortunately, there were no eggs of the last-named species available to test this bug as a possible host ; but if the Ra species is identical with the Moturiki species, the fact that adult parasites were seen on the back of a *Cantheconidea* female is evidence for this bug being a valid host.

Habits.—Each act of oviposition took rather under two minutes.

The parasite would not sting *Oechalia* eggs if *Platynopus* were offered to it at the same time. The original female from Moturiki produced an arrhenotokous generation.

Anisorcus affinis, CROTCH.—This insect was described by Crotch in 1874 from Fiji material. It is the commonest Coccinellid found on coconuts in Fiji—hardly a tree being without one or two individuals. The native name for it is " baroga."

On more than one occasion it has been claimed that this insect is predatory on the eggs of *Levuana* (cf. A. M. Lea, *loc. cit.*).

On small trees in Suva we have ourselves seen an adult *Anisorcus* eating eggs of *Levuana*, but it has never been absolutely certain that the eggs were not previously damaged first by some other cause and that the beetle was not acting as a scavenger.

In captivity we tried without any success to feed the beetle with healthy *Levuana* eggs. Although it fed readily on *Aspidiotus destructor*, it cannot be exclusively a scale feeder because it is found too often on trees completely lacking in scale insects. We think, therefore, that this insect subsists almost entirely as a scavenger, and regard the records of supposed attacks on *Levuana* with considerable doubt.

It certainly plays no part whatever in controlling *Levuana* even if it does at times actually destroy an occasional egg-mass.

Chelisoches morio, FABR.—This large black earwig is the commonest earwig in Fiji. It is widely distributed in the tropics.

Simmonds considered that it might attack *Levuana* in certain stages, and although we have no direct observation of such an occurrence taking place, experiments with the insect in captivity suggest that in view of its occurrence in such large numbers on certain trees that it may occasionally attack the larvae and pupae of *Levuana*.

The eggs are laid in a compact cluster in the fibre and leaf bases. We have not studied the life-history. It is a nocturnal feeder, and one adult kept in captivity in a glass tube fed every night on small *Levuana* larvae. No other food was offered. Another earwig kept in captivity ate one out of six full-grown *Levuana* larvae during a day's feeding.

A male and female were kept in a glass jar for two weeks and given no other food than healthy *Levuana* larvae and pupae. The latter were untouched, although one or two of the larvae were eaten each night.

This insect is of no consequence as a predator on *Levuana* in the field, even if it does occasionally feed on it. We think it is mainly a scavenger, as it always seems to be associated with accumulations of rubbish at the base of the leaves and flowers.

6. Abnormal Mortality amongst Young Larvae.—Under the rather descriptive title of "Infantile Mortality" we have on several occasions made field notes about a rather inexplicable phenomenon.

During a normal brood of *Levuana iridescens*, there is a fairly constant mortality amongst the larvae from the time they hatch to the time they pupate. This is caused by the action of predators and climate (used in the broadest sense). So that on any coconut leaf on which eggs have been laid and larvae have fed, there is approximately the same area of small as of large feeding marks, because the larger larvae eat more than small ones, but there are fewer of them on a leaf.

The phenomenon we refer to here is the tremendously heavy defoliation of certain leaves entirely by small feeding scars with the presence of none, or perhaps very few, of the larger scars (cf. Plate XXII, Fig. A, and Plate XXIII, Fig. A). We have the following records of this occurrence :—

1. *Nasese, February* 1926.—Leaf 2 on a young tree had 5 per cent. of the leaf surface defoliated. The small scars were so numerous that it was estimated that at least 1,000 eggs must have been laid on the leaf, whereas large scars were so uncommon that at a very liberal estimate not more than 100 larvae had reached the pupal stage. Other leaves on the same tree had a more normal occurrence of feeding scars. No living *Levuana* was found on this tree, so that whatever was responsible for the heavy mortality amongst the young larvae was the cause of the eradication of the moth from this tree.

2. *Naigani, October* 1926.—Leaves 12 and 13, on a tree with the first nine leaves free from signs of *Levuana*, had a preponderance of minute feeding scars. They were 15 per cent. and 35 per cent. defoliated respectively.

Other leaves with *Levuana* scars had normal occurrence of large and small scars. No living *Levuana* on the tree. This was a parallel case to that described in 1, only the cleaning up took place four or five months before the observation was made and the tree was a tall one (70-ft. trunk) in the centre of a large area of coconuts, all of which had been completely defoliated by the moth a year previously.

3. *Malamala* (*Yasawa group*), *September* 1926.—This was the most striking case met with, and we quote the circumstances in full.

A tree 30 ft. high was cut down. The first nine leaves had no *Levuana* on them. Leaf 10 had only 2 per cent. surface defoliation, half of which was done by a large number of minute scars mostly made by first-stage larvae. Such scars were present on every leaflet. Leaf 11 had 3 per cent. surface defoliation with again a great predominance of small scars. Leaves 12 to 20 had increasing defoliation from 15 per cent. to 85 per cent. respectively, and on each leaf small scars were as extremely abundant as large scars were scarce. The oldest four leaves on the tree (Nos. 21 to 24) averaged about 70 per cent. defoliation but had a higher percentage of large scars.

No living *Levuana* was found on this tree. On another tree, 100 yds. from the first, the first seven leaves were clean ; the defoliation of the remaining fourteen leaves ranged from 1 per cent. to 98 per cent. On this tree the proportion of small scars and large scars was normal.

4. *Toberua, April* 1927.—On one of the few trees on which *Levuana* was

still feeding at this time five out of twenty-three of the leaves, with old scars and no living larvae, had definite signs of extensive young larval mortality. The other leaves had a normal occurrence of scars. These five leaves were Nos. 8, 15, 16, 17 and 20 on the tree, so they represent more than one instance of mortality.

5. *Wainibokasi, May* 1927.—The twentieth leaf of a 30-ft. tree, with *Levuana* still active on the newest leaves, was 70 per cent. defoliated, almost entirely by small larvae. The photograph shown in Plate XXIII was taken of a portion of the leaf and, when compared with that of a normal *Levuana* leaf in Plate XXII, shows the very striking appearance of the small scar defoliation.

Several more instances of the same phenomenon have been noticed from time to time, details of which were not noted down ; it is, in fact, of quite common occurrence, and we feel very dissatisfied that we have never with certainty been able to attribute a cause to this abnormal leaf scar distribution. The few cases quoted above show that it occurs in both the wet and dry zones, so that it is unlikely to be caused by a climatic factor. Young larvae dying in large numbers on a leaf have never been seen, so we are ignorant whether it is caused by a bacterial or fungus disease.

A possible explanation is that on certain occasions ants have removed all the small larvae on a certain leaf or tree. Such a view is not unreasonable, when one remembers the purely incidental and irregular way in which many ants make predatory attacks.

In certain cases it might be argued that a preponderance of small scars on one leaf was merely the result of the particular leaf being loaded to excess with egg-masses. Had the leaves displaying this preponderance been completely defoliated, the explanation would have been reasonable, as the larvae would have been compelled to feed on other leaves during their later stages ; but as will be seen from the above quoted instances the defoliation was in many cases not more than 30 per cent. of the total leaf surface ; so that, taking into consideration the fact that only a small percentage of larvae migrate from one leaf to another unless compelled to by food shortage, some lethal factor must have decimated the numbers of larvae before they were half grown.

7. Fungus.—In 1913 a fungus, thought to be the cause of the periodic destruction of *Artona catoxantha* in Malay, was described by Massee as *Botritis necans* (cf. Gater, 1925).

In 1914 Jepson negotiated for cultures of the fungus to be sent to Fiji. Attempts to establish it proved unsuccessful.

Another importation of the same fungus was made in 1920, when Dr. A. G. Carment, Bacteriologist in Fiji at that time, made subcultures of the fungus and attempted innoculation of healthy *Levuana* larvae. None of the larvae died. An emulsion of the spores was sprayed over trees infested with the moth.

At about the time that Carment was studying the Malay fungus, Simmonds found a fungus very prevalent amongst dead pupae at Nasese where an outbreak of the moth was reaching its concluding stages.

Carment (1921) made subcultures from Simmonds's material, and after inoculating healthy *Levuana* larvae found that a considerable number of them died after spinning their cocoons. He determined the fungus as belonging to the family Entomophthoreae, but no specific determination was made. If Carment was right in his view that the fungus was pathogenic it is surprising that it had not been more widespread in the past, owing to the ideal conditions for its dissemination during the advanced stages of *Levuana* outbreaks ; but Jepson makes no mention of any indigenous fungus attacking *Levuana* up till the end of 1924. Therefore we may say that the records of fungus attack on *Levuana* were so few and indefinite that it is extremely unlikely that fungus played any important part in controlling outbreaks.

In January 1925, Tothill saw unmistakable signs of fungus attack in larvae on the coconuts at the old Government Experiment Station, Nasinu. He sent specimens to Canada for determination. Larvae were found in all stages of attack, the residue after death being merely a black smear on the leaf where a larva had been.

In May 1926, Paine found similar symptoms of fungus attack on *Levuana* larvae on some small trees beside the Bau road. Here the trees were so smothered with larvae that conditions were ideal for the rapid spread of fungus disease.

These are possibly the only absolutely definite records of fungus playing an active part in controlling *Levuana*, and we incline to the view that the fungus that occurs so commonly in old pupal masses is a saprophyte feeding on the corpses of moths that have died in their efforts to force a passage through a mass of cocoons.

8. Infertile Eggs.—We have already referred to the occurrence of infertile eggs. From the point of view of natural control, their occurrence is so limited that the effect is negligible. On only one occasion were infertile eggs at all common (Makuluva, 1/28) ; and even then at a very liberal estimate not more than 5 per cent. of the eggs laid were in this condition. Usually the percentage is probably less than one.

9. Parasites.—There are no records of any parasites having been bred from either the eggs or larvae of the moth prior to 1925, although an exceedingly large number of individuals had been examined.

Mr. A. M. Lea (1924), who spent a few months investigating *Levuana* in 1924, states that : " Several Dipterous and Hymenopterous parasites have been reared from the pupae." This statement seems rather an exaggeration, unless he mistook the Phorid fly, *Apiochaeta scalaris*, which breeds frequently in dead pupal masses and is a well-known scavenging insect, for a true parasite Neither he nor any other observer had bred a Dipterous parasite from any stage of *Levuana*. Hymenopterous parasites have on only three occasions been bred from *Levuana* pupae, and two of these instances occurred after Lea's observation was made. We have Lea's specimen of a parasitised pupa in our collection. Apart from the fact that the parasite was a Chalcid (*sens. str.*), which died after maturing inside a pupa of the moth, the specimen was too much disintegrated by mildew to allow of any further determination being made.

Another very similar instance was met with on the Ra coast in June 1925, the remains of a Chalcid—about the same size as that found by Lea—being found inside a dead *Levuana* pupa.

In the other instance of parasitism which occurred on material collected in Suva, a medium-sized adult female Chalcid emerged from a pupa of *Levuana*. This Chalcid appeared to be identical with a species of *Brachymeria*, a common primary pupal parasite of *Agonoxena argaula*. Owing, however, to an unfortunate accident, the insect escaped from the tube in which it emerged, and we were unable definitely to establish its identity. We have the *Levuana* pupa with a typical Chalcid emergence hole in our collection in Suva.

True parasites, therefore, played no part whatsoever in the natural control of the moth prior to the introduction of *Ptychomyia remota*.

THE TACHINID FLY, PTYCHOMYIA REMOTA, ALDRICH

SYSTEMATIC

THE fly (see Plate XXXII) was described by Dr. J. M. Aldrich, Custodian of Diptera in the United States National Museum, from a long series of adults sent from the Federated Malay States by Mr. B. A. R. Gater. The original description is as follows :—

"Resembles *Ptychomyia selecta*, Meigen, type of the genus, in size and the following characters (I have only the female of *selecta*, one European specimen determined by Brauer and Bergenstamm, for comparison) : eyes and parafacials bare ; ocellar bristles proclinate, far apart, located a trifle below the level of the anterior ocellus ; third antennal joint long, nearly five times the second in the female, penultimate joint of arista about three times as long as thick ; facial ridges with strong, erect bristles almost up to arista ; facial depression deep ; bucca (below eye) narrow. Third vein with strong setules at base, usually extending nearly to the cross-vein. Four dorso-centrals, three sterno-pleurals ; mid tibia with two bristles on outer front side, the upper one smaller ; hind tibia with irregular row on outer extensor side ; female with last abdominal segment in the form of a short blunt cone.

"Differs from *selecta* in having yellow palpi, a pair of small apical scutellars directed backward besides the three lateral ones ; no discal abdominal macrochaetae.

"Colour black, except palpi. Front in both sexes 0·31 of the head-width (two males and two females all measured the same by micrometer) ; parafrontals, mesonotum and basal half of abdominal segments 2–4 with golden-yellow pollen ; parafacials silvery, at narrowest less than half as wide as third antennal joint ; bucca hardly one-tenth of eye height ; frontal bristles rather far apart, only about seven in number, the lowest almost meeting the row on facial ridge. Apical half or more of abdominal segments 2–4 shining black, the basal pollinose bands interrupted in middle.

"Length 4·5 to 5 mm.

"Type. Male, Cat. No. 27,739, U.S.N.M." *

The Adult Fly.—In size and colour (see Plate XXXII) *Ptychomyia remota* resembles the smaller species of house-fly in Fiji. It may be distinguished from the latter insect by the presence on the body of large black bristles, and by the bare arista of the antenna, if examined with a lens.

Moreover, when the fly is in an attitude of rest the wings meet at a greater angle than do those of the house-fly.

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* Reprinted from the *Proceedings of the Entomological Society of Washington*, xxvii, No. 1, January 1925.

The fly does not visit houses or fly to a light at night, so that it is very unlikely that specimens will be seen unless met with out of doors in a locality near a host.

The sexes can be most readily distinguished, as in the case of most Tachinids, by the presence in the female of the two proclinate orbital bristles (see Plate XXXII), and although old specimens become denuded, the scars of the bristles still show. These bristles are wanting in the male.

The abdomen of the female is not especially modified in connection with ovipositing; the ovipositor is short.

There is nothing remarkable about the internal genitalia, but we have figured those of each sex (Figs. 105 and 106).

Range

Known at present from the Federated Malay States and Java. Probably occurs throughout the range of *Artona catoxantha.*

Hosts

* Gater records three insects as hosts of *P. remota* in Malay :—

1. *Artona catoxantha*, Hamps.
2. *Achaea janata*, L.
3. *Sylepta derogata*, F.

Taylor reared it in Java from

4. *Artona trisignata*, Snell.

In Fiji the following insects have been attacked by the fly in the field :—

5. *Levuana iridescens*, B-B.
6. *Plutella maculipennis*, Curt.
7. *Eublemma* sp.

The fly has also been bred through on the following insects in the laboratory, but we have no record of attacks on these insects in the field :—

8. *Callimerus arcufer*, Chap.
9. *Agonoxena argaula*, Meyr.
10. *Sylepta derogata*, F.

Eggs of *P. remota* have been found on the following insects in the field, but we have never succeeded in rearing the fly on any of them :—

1. *Rhesala* sp. (feeds on *Tournefortia argentea*).
2. *Terias hecabe*, L.
3. Larvae of an undetermined moth which feeds on *Sophora tomentosa.*
4. *Graeffea cocophaga*, Newp.

Adult flies in captivity laid eggs on larvae of *Nacoleia octosema*, the Fijian Banana Scab Moth; but none of the issuing maggots succeeded in boring into these caterpillars.

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* *Malayan Agric. J.*, xiii, 1925, p. 113.

We feel quite assured that there are many more hosts in Fiji which have not been found, owing to the abundance of the fly in localities where the hosts enumerated above were absent previously. And as the fly was bred through on a larva of *Callimerus arcufer* on three separate occasions, it is probable that its range of hosts in the field is not limited to Lepidoptera.

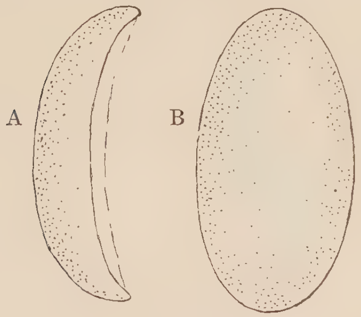

FIG. 86.—A. Dorsal view of egg of *Ptychomyia.* Under a ⅔ in. objective the chorion appears white and structureless. Length 0·5 mm., greatest width 0·25 mm. B. Lateral view of the same egg. The ventral surface is concave.

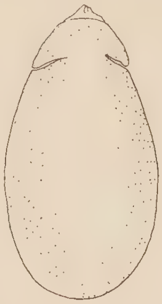

FIG. 87.—*P. remota.*—Dorsa view of egg after hatching of maggot. Showing point of dehiscence at anterior end, and portion of ventral membrane protruding from anterior end of egg. × 106.

Description of the Early Stages.—*The Egg* (Fig. 86).—White and glossy on the upper surface which is strongly convex ; chorion structureless.

Outline varying from subeliptical to oval, the micropyle being at the narrower end.

Maximum width at three-fifths the length from the micropylar end.

Rather flattened dorso-ventrally with slight longitudinal curvature. At eclosion the upper surface of the egg becomes split transversely on either side at the anterior end (see Fig. 87).

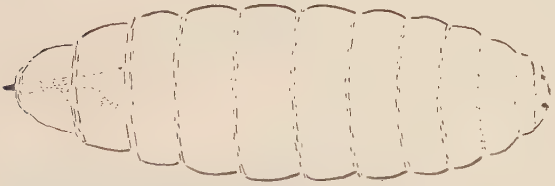

FIG. 88.—Dorsal view of first-stage larva of *Ptychomyia.* This larva has recently hatched and is 0·6 mm. long. An older one nearly ready to moult measured 1·3 mm.

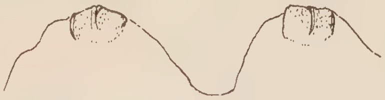

FIG. 89.—*P. remota.* — Spiracles (posterior) of first-stage larva. × 680.

Length	0·50 mm. (max. 0·53, min. 0·48)
Width	0·28 mm. (max. 0·30, min. 0·25)

First-stage Larva (Fig. 88).—Cylindrical, caudal segments simple, not especially truncate. Thirteen visible segments, including head ; the intersegments rather indistinct at the posterior end.

Posterior spiracles inconspicuous (Fig. 89), opening slightly ventrad of the median axis.

Anterior spiracles absent.

Ambulatory spinules present on the anterior part of every segment; extending right round the body, but not so well developed dorsally; largest in the two anterior segments, where they consist of minute, backwardly directed spines arranged in irregular rows extending back over the anterior third of the segment. The spinous nature of the processes becomes less marked posteriorly; but on the caudal segment there is a band of rather larger forwardly directed spinules. In addition to the transverse bands of spinules there are groups, each with two to five larger, forwardly directed spines of irregular shape, on the mid-lateral line of the body. Each segment in the central part of the body being armed with one group.

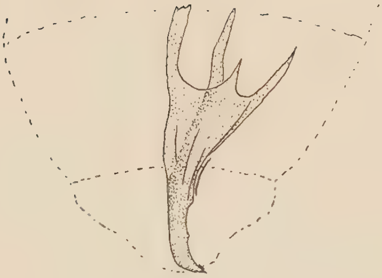

Fig. 90.—*P. remota.*—Lateral view of pharyngeal skeleton of first-stage larva. × 440.

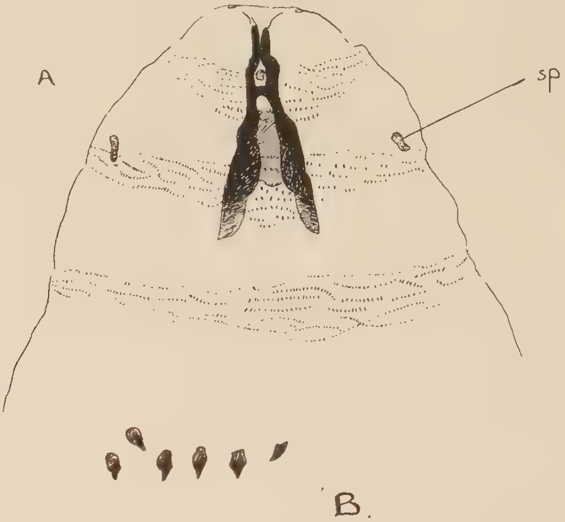

Fig. 91.—*P. remota.*—A. Ventral view of anterior segments of second-stage larva: showing pharyngeal skeleton anterior spiracles (*sp.*) and three bands of ambulatory spinules. B. An enlarged drawing of some of the spinules from the third segment.

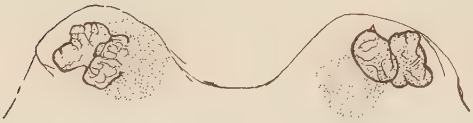

Fig. 92.—*P. remota.*—Spiracles (posterior) of second-stage larva. × 300.

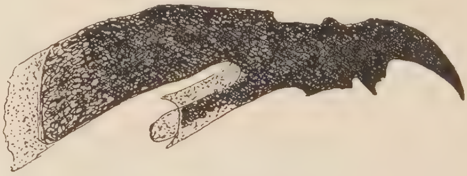

Fig. 93.—*P. remota.*—Pharyngeal skeleton of second-stage larva: lateral view. × 250.

The pharyngeal skeleton (Fig. 90) consists of an unpaired hook, bifurcating posteriorly: extending to the anterior margin of the third segment.

There is a small sensory pit on either side of the oral cavity.

Size when newly hatched 0·6 mm.; when fully grown 1·5 mm.

Second-stage Larva (Fig. 91).—Shape as in first stage; maximum width at seventh segment. Posterior part of body usually curved slightly upwards. Tracheal trunks conspicuous in a dorsal view.

Posterior spiracles situated a little dorsad of the median axis: feebly chitinised; showing as two brown spots: each with two breathing pores (Fig. 92) and opening at the extremity of a slight prominence of the caudal segment; the surrounding area of integument is slightly retracted, so that the spiracles do not necessarily project beyond the posterior profile of the body.

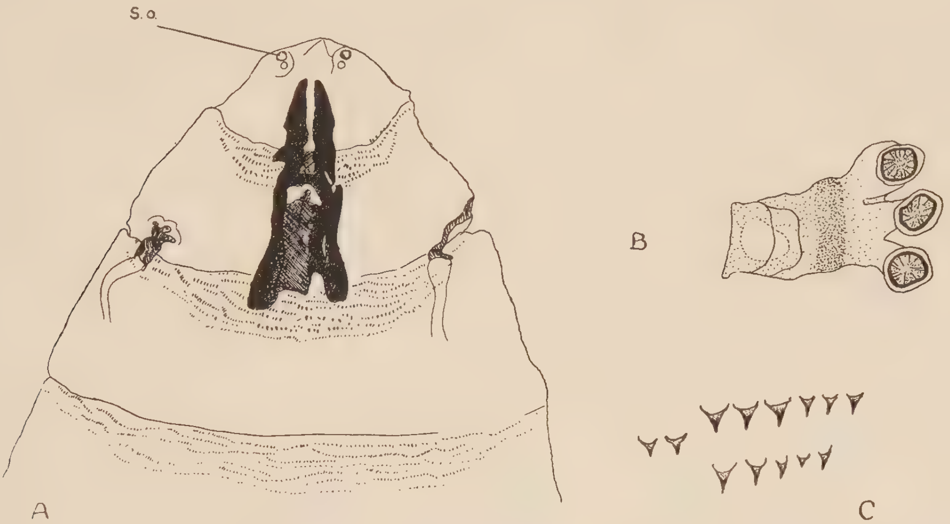

Fig. 94.—*Ptychomyia remota*, Ald. Third-stage larva. A. Ventral view of anterior segments to show ambulatory spinules of pharyngeal skeleton and sensory pits (*s.o.*). B. Enlarged view of anterior spiracle showing the three external pores. C. Ambulatory spinules from the median area of the third segment.

Anterior spiracles present, but small (Fig. 91, A. sp.), situated laterally at the junction between the second and third segments: functionless. Sensory pits beside the oral cavity as in first-stage larva. Ambulatory spines largest on the venter of the two anterior segments; arranged in a series of rows. They are all backwardly directed in the anterior part of the body; but in the central part they are smaller, and in some rows project forwards. Caudally the spinules are almost all directed forwards.

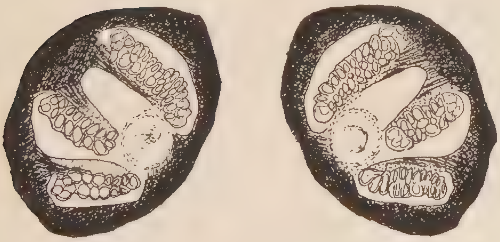

Fig. 95.—*P. remota.*—Spiracles (posterior) of third-stage larva. × 250.

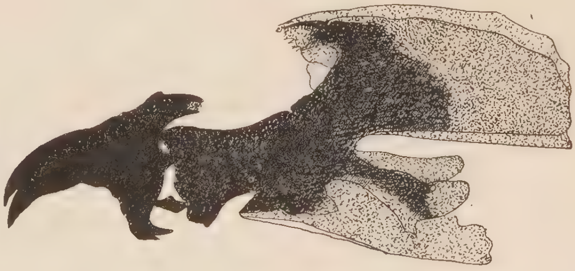

Fig. 96.—*Ptychomyia remota.*—Lateral view of pharyngeal skeleton of third-stage larva. × 250.

Except for a small chitinous connection at one-third the length from the anterior end, the pharyngeal skeleton (see Fig. 93) is divided longitudinally and dorso-ventrally into two parts. The anterior hook being thus duplicated. The posterior part is tubular with the ventral surface more feebly chitinised. A longitudinal breach dorsally. No transverse divisions.

Length ranges from 1 to 4 mm.

Third-stage Larva (Fig. 94).—Shape as in other stages. Posterior spiracles heavily chitinised and pigmented, conspicuous (Fig. 95).

Anterior spiracles inconspicuous externally each with a trifid pore on the dorso-lateral aspect of the second-third intersegment. Two small sensory pits on either side of the buccal opening.

Anus not conspicuous, situated mid-ventrally on the fourth segment.

Ambulatory spines arranged as in second-stage larva. The pharyngeal skeleton (Fig. 96) is divided transversely into three closely approximated parts. Moreover, the whole structure is bilateral, as in the second stage. The anterior sclerite hooklike; middle piece small and saddle-shaped, its posterior margin fitting closely against the larger posterior sclerite to which the musculature is attached.

Length ranges from 2·5 to 7 mm.

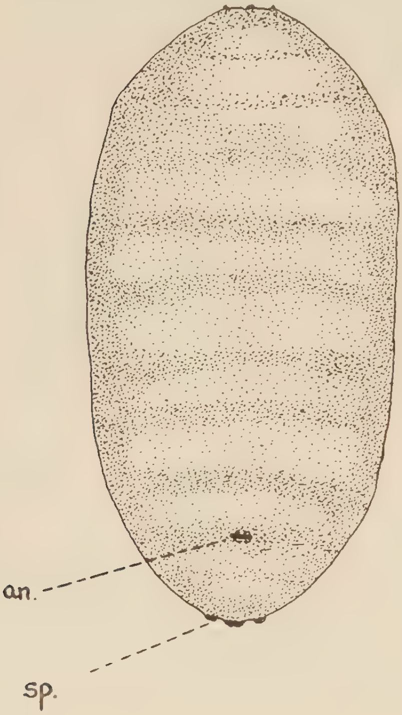

FIG. 97. — *P. remota.* — Puparium ventral view. × 20. *An.*, anus; *sp.*, spiracle.

The Puparium (Figs. 97 and 98).—This is described and figured by Gater.* His description as follows :—

"Length 4·5 mm. to 5·0 mm.: in exceptional cases the length may be only 2·5 mm. Medium to dark brown, subshining smooth, almost regularly cylindrical but inclined to taper slightly towards anal end, segmentation fairly distinct, marked by narrow bands of minute spinules at sutures. Stigmal plates shining black, slightly rugose, showing contours of ridges, slightly raised, placed just above longitudinal axis and separated by about half their own width. Slits three in number, button round, small and slightly below level of slits. On the longitudinal axis below stigmal plates, almost contiguous and forming a triangle with them, is a rounded tubercle with a crater-like depression. Anal opening located far below."

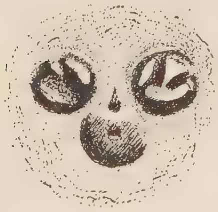

FIG. 98.—*P. remota.*—Posterior view of puparium showing spiracles and median plate. × 70.

All the puparia we have examined have been very slightly flattened dorso-ventrally in the anterior half and compressed laterally in the posterior half, so that in a dorsal view the maximum width is at one-third, and in a lateral view at two-thirds, the length from the anterior end.

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* *Malayan Agric. J.*, xiv, 1926, p. 326.

There is a minute prominence on either side of the anterior extremity about the level of the median axis.

A puparium bred from *Sylepta derogata*—a much larger host than *Levuana*—measured 5·7 mm. in length. The smallest puparium obtained from *Levuana* measured only 2·1 mm. in length. Between these two extremes, every size is met with, the average dimensions being about 4 × 2 mm. The length in all cases is about twice the width.

LIFE-HISTORY

General.—During the period (August to December 1925) when *P. remota* was being bred in captivity for colony distribution, a long series of inclusive (*i.e.* oviposition to emergence of adult) development period records were accumulated. The periods concerned varied during those months from sixteen to twenty-nine days.

The more detailed life-history was worked out during November and December 1927. Puparia were collected from the field (Makuluva), adults bred out, and a complete record of the development of the F1 generation made. The F2 generation provided additional material for some points that needed further elucidation.

The incubation period and larval stages were studied by keeping the parasitised host larvae in separate glass tubes with a daily feeding of fresh coconut leaves. Since it was noticed that any pathological condition arising in the host larva caused an abnormal, if adaptational, extension of the parasite's development, it was found necessary to give all possible care to the welfare of the host. In spite of these precautions many of the host larvae died before the maggots completed their development, and such cases are not taken into account in the tabulation of normal parasite development given in tables on pp. 191–193.

It was also discovered that the early stages of the parasite seemed to vary within such wide limits without any obvious cause that it became necessary to study carefully such factors as might possibly be influential, *e.g.* :

(*a*) The stage of host attacked.
(*b*) The number of eggs laid on each host.
(*c*) The age of the flies at time of egg laying.
(*d*) Temperature.

As a result of these observations it has been found that although there is considerable variation in the total period from egg laying to pupation, yet this is essentially due to two factors, the stage of the host attacked, and the lapse of time between successive acts of oviposition by the parent fly. The resulting variations are manifest chiefly in the incubation period and first larval stage of the parasite, and a full description of this is given under the account for the stages concerned.

As well as obtaining accurate data concerning the incubation period and larval stages, it was considered necessary to make some few records of the complete life-history for comparison with those obtained in 1925.

It was then found that a thirteen-days' (egg to adult) development was not uncommon—the pupal period in each case being approximately eight days. This is three days shorter than the minimum recorded in 1925.

Gater * (1926) has shown by experiments with a multiple-temperature incubator that the pupal stage of *P. remota* can be considerably lengthened by keeping pupae at temperatures a few degrees lower than the mean outside temperature for Malaya. Therefore it would seem that the shorter period of development observed in the recent set of breeding experiments was due to an accelerated pupal period, the mean maximum and minimum temperature in the breeding room being 86·5° F. and 77° F.—a temperature several degrees in excess of that for the period August to December 1925. when the weather was comparatively cool for the time of year, and when the breedings were carried out in large cages often kept out of doors. This seems a more reasonable conclusion to adopt as an explanation of the difference noted than to suppose that it were caused by either of the factors mentioned above which contribute to individual variations ; because, in the cages in 1925, hosts of all stages and flies of all ages were used and a very large number of records made.

In view of this, it has not been considered necessary to make a large number of records of the pupal period, especially as it is not influenced in any way by such factors as the stage of host attacked, etc. ; therefore in the tables appended pupal periods are omitted.

It was at first considered necessary to dissect all host larvae in order to discover the stage of the parasite, but subsequently it was found possible to ascertain this in many cases by examining *in situ* the spiracles of the parasite, which are quite characteristic for the three larval stages.

In doubtful cases dissection was always resorted to, but it was only necessary on such occasions, as when the maggot was feeding so low down in the funnel that there was insufficient light to see the spiracles ; or when the latter were obscured by the curvature of the funnel ; or again, in cases of superparasitism, when there are several funnels closely approximated.

The spiracles of the third-stage maggot are seldom visible down the funnel except just after the second moult, because the larva in that stage ruptures the funnel and feeds indiscriminately on any part of the host. But hosts with third-stage larvae inside are always dead and have a characteristic appearance, and if prodded gently, display the movements of the contained maggot, so that there is no difficulty in the determination of this stage.

Altogether records of nearly thirty larvae which completed development were made ; but in the table on p. 192, the majority of the records had to be made by dissections.

A record was kept of all cases of superparasitism, and a separate account of it is given in the sequel ; let it suffice to say here that since this phenomenon has no appreciable effect on the periods taken for the various stages, it has been considered simpler to make a separate table (see pp. 192, 193) of those host larvae which display it, and use the records more for study of the behaviour of the various parasites than for a mere record of time factors.

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* *Malayan Agric. J.*, vol. xiv, 1926, p. 337.

Incubation Period.—The period between the laying and hatching of the eggs of *P. remota* varies between comparatively wide limits. This variation is in no way an adaptation to the condition of the host; it is due to the fact that under certain conditions fertilisation of the ovum is not immediately followed by oviposition, so that development of the embryo proceeds within the uterus of the parent, which, in extreme cases, may result in larviposition.

On the other hand, an abnormal incubation period may take place, for in the course of the recent experiments eggs were laid that took more than fifty-five hours to hatch; but in all such cases the larvae which emerged were pathological and died before attempting to bore into the host. Such eggs were laid in captivity by flies which would be laying perfectly normal eggs at other times, and since there was nothing to indicate that this lengthening of the incubation period was due to the condition of the host or to any ill effect caused by the hatching of other eggs on the same host (many of the cases observed being on hosts with only one egg), we must conclude that it is an abnormal condition the cause of which is concerned with the development of the ovum inside the parent.

Therefore, taking into account all cases observed of eggs which were fertile, the incubation period, external to the body of the parent, varied from half an hour to 100 hours. But excluding from the reckoning the abnormally long and pathological cases referred to above (as has been done in the appended tables), the typical incubation period of the egg, whether or not it occurs partly inside the parent, varies between thirty-six and fifty hours, with the great majority of cases at about forty hours.

It is necessary here to say something concerning the occasional development of the fertilised egg inside the body of the parent.

Since no cases of oviposition have actually been observed in the field, all the records of incubation periods have been made with flies kept in captivity. In order to obtain a precise knowledge of the exact period of oviposition for a large number of eggs laid by a few flies, it was necessary to keep a check on the layings by placing a number of unparasitised host larvae in each fly jar for the space of but one hour at certain periods of the day: and larvae were never left in the jars overnight, *i.e.* between 5 p.m. and 8 a.m., on any day on which records were made.

It was found that among each day's eggs there were always some, never more than four, which hatched out in less than thirty hours from the time they were laid. As there were altogether four female flies in the jars, it seemed a matter of more than mere coincidence, and a further check was made of two such cases, when it was found that in each case the egg was the first laid by a female on the particular day in question. It was not possible to check this matter further by direct observation, but there seems little cause for doubt that in all such cases the eggs that hatched early were the first laid by each fly at the start of a day.

We may, therefore, suppose that the larvae placed in the jars between 4 and 5 p.m. excited the flies to oviposition, and the preceding act of ejecting spermatozoa into the uterus, and that when the host larvae were all removed at 5 p.m. it often happened that some flies had eggs already fertilised inside them with no available host on which to lay. Development of the embryo must in such cases proceed inside the body of the parent, and when, in one instance, opportunity to oviposit was not renewed until after the lapse of some forty-five hours, it was found that the egg hatched within half an hour of oviposition. Further evidence to support this view is that in one fly, which was dissected after being starved of host material for more than two days, a first-stage maggot was found in the uterus beside the egg from which it had hatched, and the next succeeding egg showed no sign of any embryonic development, and had obviously not been fertilised when the fly died.

In a column of the table shown at p. 191 will be found a record of incubation period for eggs laid on some forty *Levuana* larvae. Those eggs which took less than thirty hours to develop are marked with an asterisk, and are not included in the compilation of the summary table where the range and mean periods for the various stages are set forth.

This might at first sight seem to be drawing too arbitrary a distinction between eggs whose incubation period shows a fairly continuous range from half an hour to more than two days ; but if the incubation periods of a large number of eggs were shown by a graph, it would be found that the bulk of them vary between forty and forty-five hours, and that records of from thirty to forty hours are very scarce, whereas there is a slight increase in the number of those below thirty hours.

Thus, although the distinction is somewhat vague, yet it does separate into two sets, those eggs which are fertilised at the moment of oviposition and those in which the embryos have developed to a greater or less extent prior to leaving the body of the parent. Since it is considered that the latter state is induced by laboratory conditions which may not have their counterpart in natural surroundings, it has been considered advisable to maintain the distinction.

The Larval Stages.—A range of some twelve days was noticed between maximum and minimum egg to adult periods ; this is mainly to be accounted for by the marked variation in length of the larval period. That this variation is not entirely a haphazard matter, but an adaptation to the condition of the host, may be seen by referring to the records set forth in the table (p. 191), in the right-hand column of which is expressed the total larval period taken by each of the twenty larvae whose development was studied in full.

These periods are divisible into three groups, namely :

(*a*) Those which range from seven to twelve days (Nos. 2, 3, 22, 23, 24, 25, 26, 27, 35 and 36).

(*b*) Those which average about four and a half days (Nos. 5, 6, 7, 8, 32, 37, 40 and 42).

(*c*) Those which exceed twelve days (Nos. 4 and 31).

To group (*a*) belong the cases where parasite eggs are laid on a host larva which is third or fourth stage, and which is not killed by the parasite until it has moulted once and is well advanced in the next instar. (There are, however, two exceptions to this—Nos. 35 and 36—these were both cases in which eggs were laid on larvae just after they had completed their fourth moult, and the fifth stage of the host was exceptionally long.) To this class belongs the majority of larvae which have eggs laid on them prior to the last stage.

To (*b*) belong those cases where the parasite egg is laid on a host which is unable to moult before being killed by the parasite, whose larval stages are much abbreviated. This is the rule for eggs laid on fifth-stage larvae (very few of which ever pupate) and for a small percentage of those laid on earlier stages.

To (*c*) belong those very rare cases where the host larva actually completes two moults before being killed by the parasite. (N.B.—No. 31 was one of those atypical *Levuana* larvae which have an extra instar.)

The parasite as a rule (the only exceptions here being Nos. 2, 5 and 32) " allows " the host to feed unimpeded, and it bides its time until the host has completed the instar's growth and contracts itself preparatory to a moult. When the host is in this condition it seems to be in the most suitable state for the parasite to take full possession of the situation, possibly because of the physiological changes which go on within the host before a moult, more especially that preceding pupation. With an observed 85 per cent. of such cases (including here the eight cases recorded in the table on p. 192), it must be due to some specific cause. The only question which now remains to be answered is, why are occasional larvae attacked prior to their last stage, and yet belonging to our group (*b*) ?

The only cause for this which can be suggested here is that in certain cases maggots bore into regions of their hosts where their scope for feeding without interfering with some vital organ is very limited. Under such conditions their growth might be abnormally retarded until, when their hosts reach that phase prior to a moult, which is referred to above as being especially suited to the rapid development of the parasite, they take advantage of the situation to complete their development at the expense of killing their host, thus sacrificing their chances of being provided with the more usual fully-grown host.

In the rare cases, where the host moults twice between the time when the parasite egg is laid and when the maggot reaches third stage, it seems possible that just the opposite has happened, namely, that the parasite, having access to an extensive, and from the point of view of the host unimportant, feeding ground, is able to wait until the host has grown to a maximum size before killing it.

Or perhaps a better explanation is that the parasite is not stimulated to complete its development as a larva until those far-reaching physiological changes associated with the prepupal period begin to take place within the host.

In any case without a detailed study of the physiological relationship between parasite and host, any suggestions put forward to account for these phenomena are at best of only a very hypothetical nature.

Having now studied the nature of the variability of the larval period of *Ptychomyia*, it will be convenient to refer to the larval stages, of which only three have ever been observed, under separate headings.

First Stage.—The maggot, on hatching from the egg, loses no time in boring into the host and commencing to feed. If the egg is laid so that the micropylar end is apposed to some relatively thinly cuticled part of the host integument (as is usual with larvae of *Levuana*), the maggot will bore into the host before fully emerging from the egg, and the latter is prevented from blocking the breathing chamber of the maggot by the rapid development from the host's integument of a breathing funnel which prises up the egg to a certain extent and allows free air access to the spiracles of the maggot.

It occasionally happens, however, especially on hosts other than *Levuana* (cf. Fig. 104), that when the maggot emerges from the egg it comes in contact with some heavily chitinised part of the integument, and is unable to bore in without crawling over the surface of the host to some more suitable spot. This has actually been observed with *Levuana* where eggs were laid on the heavily chitinised prothoracic hood.

The first stage is normally much longer than either of the other stages, varying from one to over twelve days—the mean being about four days (see p. 193). The reason for this is that in the numerous instances where eggs are laid on hosts that have not yet reached their final larval instar, the adaptational response of the parasite (noticed above) becomes manifest in the first larval stage when it does not interfere with any of the natural functions of the host.

Second Stage.—The duration of this stage is usually brief; and although the maggot still continues to feed within the host funnel and does not vitally damage the host (except in certain cases of superparasitism discussed elsewhere), yet this stage is not, like the first, an extensible feeding period during which the maggot awaits the full development of the host. Thus, the maximum reading for this stage in the experiments was only three days eight hours as compared with twelve days twelve hours for the first stage; and in only two cases (Nos. 14 and 37) was the second stage longer than the first of the same larva.

In those larvae which are grouped under class (*b*) (see above) the stage may be extremely short, varying from twelve to twenty-four hours in most cases.

The mean period of this stage for all the records is approximately a day and a half; and thus, once the first moult is completed, development is rapid until pupation.

Third Stage.—This is the stage when the maggot starts its destructive feeding and the host dies very shortly, in most cases less than two hours after the second moult of the parasite is completed. Furthermore, the maggot leaves the integumental funnel and works its way all over the inside of the

TABLE SHOWING DURATION OF EARLY STAGES OF *PTYCHOMYIA REMOTA* ON *LEVUANA IRIDESCENS* LARVAE OF VARIOUS STAGES.

Not more than one Parasite in each Host Larva.

	HOST.		PARASITE.									
	Stage at time of oviposition.	Stage when killed.	Incubation period.		First stage.		Second stage.		Third stage.		Total larval period.	
			Days	Hours	Days	Hours	Days	Hours	Days	Hours	Days	Hours
1	3rd	3rd moult	—		2	0	1	0	D		—	
2	,,	4th	1	22	5	15	1	10	1	17	8	18
3	,,	4th moult	1	17	4	17	2	0	1	10	8	3
4	,,	prepupa	1*	6*	11	6	3	8	1	2	15	16
5	4th	4th	1	19	2	0	1	4	1	0	4	4
6	,,	4th moult	0*	22*	1	20	0	12	1	20	4	4
7	,,	,,	1	19	2	0	1	0	1	0	4	0
8	,,	,,	1	20	2	0	1	0	1	0	4	0
9	,,	,,	0*	0·5*	3	0	1	12	D		—	
10	,,	,,	1*	0*	3	10	D		—		—	
11	,,	,,	1	22	2	2	D		—		—	
12	,,	,,	1	19	2	5	D		—		—	
13	,,	,,	1	12	D		—		—		—	
14	,,	5th	1	22	2	22	3	8	D		—	
15	,,	,,	1	18	4	19	1	0	D		—	
16	,,	,,	1	18	4	19	D		—		—	
17	,,	,,	1	18	2	2	D		—		—	
18	,,	,,	1	19	D		—		—		—	
19	,,	,,	1	20	D		—		—		—	
20	,,	,,	1	21	D		—		—		—	
21	,,	,,	1	12	D		—		—		—	
22	,,	prepupa	1	12	6	0	1	10	1	13	8	13
23	,,	,,	1	19	5	16	2	12	2	17	11	21
24	,,	,,	1	19	3	17	2	13	1	16	7	22
25	,,	,,	1	17	8	8	1	20	1	0	11	4
26	,,	,,	1	18	6	0	1	12	0	16	8	4
27	,,	,,	1	18	5	0	1	6	1	20	8	2
28	,,	,,	1	19	4	18	D		—		—	
29	,,	,,	1	20	4	18	D		—		—	
30	,,	,,	1	14	4	18	D		—		—	
31	,,	prepupa, 6th stage	—		12	12	1	0	1	0	14	12
32	5th	5th	1	18	3	0	1	0	1	0	5	0
33	,,	,,	1	19	D		—		—		—	
34	,,	,,	0	20	D		—		—		—	
35	,,	prepupa	0	19	5	0	2	0	2	4	9	4
36	,,	,,	0	16	7	20	1	0	1	0	9	20
37	,,	,,	1	18	2	0	2	4	1	0	5	4
38	,,	,,	1	18	4	14	1	16	D		—	
39	,,	,,	1	18	2	2	D		—		—	
40	prepupa	,,	—		2	0	1	0	1	0	4	0
41	,,	,,	0	20	1	3	1	0	D		—	
42	,,	pupa	1	20	2	0	1	0	1	0	4	0

* Not included in the summary table because abnormally short.
D. Indicates host dissected to examine parasite.

TABLE SHOWING DURATION OF EARLY STAGES OF *P. REMOTA* ON *L. IRIDESCENS* LARVAE OF VARIOUS STAGES WHEN SUPERPARASITISM HAS OCCURRED.

I.e. More than one Parasite Egg Laid and Hatched on each Host Larva.

	Host.		Parasite.				
	Stage at time of oviposition.	Stage when killed.	Incubation period.	First stage.	Second stage.	Third stage.	Total larval period.
			Days Hours	Days Hours	Days Hours	Days Hours	Days Hours
1 (*a*)	4th	4th	0 21*	3 18	(1 12 D)	—	—
(*b*)	,,	,,	1 19	2 22	•	—	—
(*c*)	,,	,,	1 19	2 22	•	—	—
2 (*a*)	4th	4th moult	1 18	2 0	1 4	2 0	5 4
(*b*)	,,	,,	1 18	•	—	—	—
3 (*a*)	4th	4th moult	1 19	1 4	0 20	1 10	3 10
(*b*)	,,	,,	1 19	1 21	•	—	—
4 (*a*)	4th	4th moult	1 21	1 6	0 22	1 0	3 4
(*b*)	,,	,,	1 8	2 16	•	—	—
(*c*)	,,	,,	1 21	1 6	•	—	—
5 (*a*)	4th	4th moult	1 22	1 4	0 20	(0 4 D)	—
(*b*)	,,	,,	1 22	•	—	—	—
(*c*)	,,	,,	1 22	•	—	—	—
(*d*)	,,	,,	1 22	•	—	—	—
(*e*)	,,	,,	1 22	•	—	—	—
6 (*a*)	4th	4th moult	1 22	1 20	(0 12 D)	—	—
(*b*)	,,	,,	1 22	•	—	—	—
(*c*)	,,	,,	1 22	•	—	—	—
(*d*)	,,	,,	1 22	•	—	—	—
(*e*)	,,	,,	1 22	•	—	—	—
(*f*)	,,	,,	0 22*	•	—	—	—
7 (*a*)	4th	4th moult	1 12	(1 0 D)	—	—	—
(*b*)	,,	,,	1 12	(1 0 D)	—	—	—
8 (*a*)	4th	5th	2 5	4 9	(0 12 D)	—	—
(*b*)	,,	,,	1 21	5 22	•	—	—
(*c*)	,,	,,	2 0	•	—	—	—
9 (*a*)	4th	prepupa	1 13	5 17	1 22	0 12	8 3
(*b*)	,,	,,	1 13	•	—	—	—
(*c*)	,,	,,	1 13	•	—	—	—
(*d*)	,,	,,	1 13	•	—	—	—
10 (*a*)	4th	prepupa	1 16	7 1	2 22	0 20	10 19
(*b*)	,,	,,	1 16	7 1	•	—	—
11 (*a*)	4th	prepupa	1 18	6 16	1 20	1 12	10 0
(*b*)	,,	,,	1 18	•	—	—	—
12 (*a*)	4th	prepupa	1 17	5 20	1 6	1 0	8 2
(*b*)	,,	,,	1 19	5 18	•	—	—
13 (*a*)	4th	prepupa	1 20	4 18	1 6	(0 6 D)	—
(*b*)	,,	,,	1 20	5 16	•	—	—
14 (*a*)	5th	5th	1 18	7 6	1 22	(0 6)	—
(*b*)	,,	,,	1 18	7 6	•	—	—

TABLE SHOWING DURATION OF EARLY STAGES OF *P. REMOTA* ON *L. IRIDESCENS* LARVAE OF VARIOUS STAGES WHEN SUPERPARASITISM HAS OCCURRED—*continued.*

	HOST.		PARASITE.									
	Stage at time of oviposition.	Stage when killed.	Incubation period.		First stage.		Second stage.		Third stage.		Total larval period.	
			Days	Hours	Days	Hours	Days	Hours	Days	Hours	Days	Hours
15 (*a*)	5th	5th	1	21	1	16	1	10	1	20	4	22
(*b*)	,,	,,	1	21	•		—		—		—	
16 (*a*)	5th	5th	0	17*	2	16	(0	12 D)	—		—	
(*b*)	,,	,,	1	18	1	18	•		—		—	
17 (*a*)	5th	5th	1	19	1	15	1	16	(0	6 D)	—	
(*b*)	,,	,,	1	19	1	15	•		—		—	
(*c*)	,,	,,	1	19	1	15	•		—		—	
18 (*a*)	5th	5th	1	0*	2	15	(1	14 D)	—		—	
(*b*)	,,	,,	1	18	2	0	(1	8 D)	—		—	
(*c*)	,,	,,	1	18	2	20	•		—		—	
(*d*)	,,	,,	1	18	2	6	•		—		—	
(*e*)	,,	,,	1	18	2	20	•		—		—	
19 (*a*)	5th	5th	1	0*	3	15	(0	12 D)	—		—	
(*b*)	,,	,,	0	21*	3	18	•		—		—	
20 (*a*)	5th	prepupa	0	22*	2	0	2	0	—		—	
(*b*)	,,	,,	0	22*	3	17	•		—		—	
(*c*)	,,	,,	1	20	2	13	•		—		—	

* Not included in the summary table.
D. Indicates host dissected to examine parasite.

EXPLANATION OF SUPERPARASITISM TABLE.

• Indicates the stage reached by the unsuccessful maggot or maggots when killed by a successful maggot in the same host.

Figures in brackets indicate the incomplete period of the stage of a living parasite at the time a dissection was made of the host.

Incubation periods of abnormally short duration, *i.e.* thirty hours or less, are marked with an asterisk.

For further explanation, see references in text.

TABLE SHOWING SUMMARY OF DATA DERIVED FROM THE TWO PREVIOUS TABLES.

	MAXIMUM.				MINIMUM.				MEAN.			
	Days	Hours	Days	Hours	Days	Hours	Days	Hours	Days	Hours	Days	Hours
Incubation period .	1	22	2	5	1	12	1	8	1	19	1	19
First stage . . .	12	12	7	6	1	3	1	4	4	3	3	11
Second stage . .	3	8	2	22	0	12	0	20	1	13	1	13
Third stage . . .	2	17	2	0	0	16	0	12	1	7	1	6
Total larval period .	15	16	10	19	4	0	3	4	7	20	6	17

host, the air connection with the exterior being maintained through the funnel which leads into the cavity of the host in which the parasite is feeding.

In only two out of twenty-eight observed cases did this stage exceed two days in duration; the maximum obtained being two days seventeen hours. It is usually much shorter than this, and some 50 per cent. of the larvae took only about twenty-four hours—the minimum being twelve hours.

The mean period for all records was about thirty hours, some six hours shorter than the time for the second stage.

After the larva has finished the food supply, it nearly always ruptures the skin of the host and crawls out to pupate, leaving a characteristic roundish hole in the integument of the host. In a few cases pupation takes place within the carcase of the host. This is particularly noticeable in those rare cases where pupation of the host has taken place.

In natural surroundings, *i.e.* beneath the cocoon of the host, the issuing maggot usually pupates against the skin of the host without breaking out of the cocoon; but when kept in glass tubes they usually crawl about after leaving the host in search of a suitable place to pupate—often making a "lair" in the cotton wool plug. But in all cases pupation succeeds the emergence from the host almost immediately.

It is worthy of note that one second-stage and numerous third-stage larvae "pupated" after they were put into a 5 per cent. solution of chloral hydrate without being previously fixed.

The Pupal Period.—It takes only a few hours for the puparium to form after the third-stage larva has settled into the characteristic contracted position.

The duration of the pupal stage seems to be very largely governed by temperature, as has been referred to above, so that these few records, all made during December 1927, must not be regarded as average for the whole year.

The larvae were kept under observation after they had left their hosts, and from all of the puparia formed, flies emerged on the eighth day. But as one did not pupate until the evening, the actual period was eight days in nine cases, and seven and a half days in one case. This, with a mean temperature of 82° for the period in question, may be taken as the minimum for Fiji. In the winter months it is probably prolonged to ten or more days, for during August and September 1925 the pupal period in a very large number of observed cases varied between nine and a half and eleven days.

Adult Life.—The only observations which have been made on this point were cases of flies kept in captivity and fed with diluted honey.

In the absence of food both sexes die within three days of emergence.

The following instances of adult life have been noted :—

Females 10 days
10 ,,
13 ,,
8 ,,
} *Mean* 10 *days.*

In all these cases there were abundant opportunities for the flies to complete oviposition during the first week after emergence. This they did in most cases; and it seems probable that had they not been able to lay all their eggs so quickly their length of life would have been greater (cf. Gater, *loc. cit.*, p. 329).

It has previously been stated (cf. Gater, *loc. cit.*) that the males die shortly after copulation. This has not been the case in our experiments. The four instances quoted above were all for flies which mated shortly after emergence.

Gater (*loc. cit.* 1926) conducted a set of experiments on adult life by feeding flies on several different foods. The maximum length of life obtained was thirty-two days, although the average for a large number of individuals was only four and a half days. Diluted honey was found to be the best food.

Summary of Life-history.—Records for August to December 1925 show that the total period taken by the early stages of *Ptychomyia* ranged from sixteen to twenty-nine days; whereas in December 1927 the range was from thirteen to twenty-six days.

The incubation period is about forty hours in most cases; the larval stages, more particularly the first, are variable between wide limits, depending on the stage of development of the host at the time of oviposition. The pupal stage is dependent on temperature and has a normal range of from eight to eleven days. The adult lives for at least ten days and probably longer under natural conditions.

Habits and Behaviour.—Adults

Feeding.—The adult fly feeds on various plant blossoms in the field. They have been found visiting the following plants :—

Mikania scandens ("Mile-a-minute"), *Tournefortia argentea*, and *Cordia subcordata*.

Habits of Flight.—*P. remota* is a most active flier, and its powers of dispersal are quite astonishing. Its very rapid spread in Fiji at the end of 1925, which is discussed at p. 27, involved a flight of at least twelve miles over water in one instance.

Mating.—Mating occurs normally during the first two or three hours after emergence of the female. In certain cases males have refused to mate with a virgin female on the first day of her adult life, but this seems to be the exception rather than the rule.

In large cages the males seem to experience some difficulty in finding the females, because it has been observed on several occasions that when pairs were confined in tubes copulation immediately took place, notwithstanding the fact that the flies had been together in the same cage for more than a day.

A male which had been alive for fifteen days inside a glass jar refused to mate with a newly emerged female. Except for this record, nothing is known as to the length of time the male organs remain efficient.

The period in copula was from five to ten minutes for three cases recently observed. Other flies observed in October 1925 took about fifteen minutes to perform this function.

Repeated copulation has not been observed. In most cases it appears to be unnecessary, as fertile eggs are laid right up to the time the female dies. But in one case a female, which had been laying fertile eggs, started to produce sterile eggs and continued laying such eggs until she died with an empty ovary.

It is not known how many females one male is capable of fertilising, but in one instance a single male fly mated with three females in the space of an hour.

Oviposition.—1. *Age of Adults at Commencement of Oviposition.*—At the earliest, oviposition commences forty-eight hours after emergence from the puparium. Larvae were offered to newly emerged females which had mated, and no eggs were laid until the second day (kept in glass jars).

Records in the breeding cages indicated a period of from three to four days after emergence.

The discrepancy probably lies in the fact that copulation immediately succeeded emergence in the case where the flies were kept in a confined space, whereas in the cages it is probable that many females did not mate until a day or more after emergence.

An unmated female kept in a glass jar refused to oviposit on the fourth day after emergence, which bears out the above hypothesis.

2. *Time of Day.*—Oviposition occurs at all times of the day (and night in artificial light) when suitable hosts are available. The death of the female seems to occur not longer than two or three days after exhaustion of the ovaries; thus the length of life of adults must depend largely on the supply of suitable objects on which to oviposit.

3. *The Act of Oviposition.*—The act of oviposition is a rapid one. It usually takes less than a second for the female fly to dart at the host, lay her egg, and then fly off. Only occasionally does a female fly actually settle on the host prior to oviposition. Flies may often be seen to settle on larvae, and in such a position they may even apply their ovipositor to the host, but it is only very seldom that an egg is laid at such a time.

4. *Rate of Oviposition.*—A space of about two minutes must occur between successive acts of oviposition by one fly. As a rule, if left to their own devices, they wait for three or four minutes between each act of oviposition; but flies "tempted" with crawling larvae in cages will endeavour to oviposit more rapidly; but it must require at least two minutes for the egg to pass from the inner end of the uterus to the base of the ovipositor, for never has egg-laying occurred (so far as captivity observations go) with less than a two-minutes' interval between each act.

When a constant supply of suitable host material for the flies is available, they space out their acts of oviposition; but one female (in a jar) which had no larvae placed with it for thirty-six hours proceeded to "pump out" eggs with extraordinary rapidity when larvae were again offered to it, and laid no less than seventeen eggs in the space of an hour, an average rate of one every three and a half minutes.

5. *Selection of Position on Host.*—The primary instinct of the fly is to place its eggs right against the skin of the host—its habits at oviposition preclude any alternative opinion (this is discussed elsewhere). This being so, it becomes a purely hazardous matter on what part of an entirely smooth-skinned host the eggs are laid; but as we are essentially dealing with the habits

of the fly as a parasite of *Levuana*—its favoured host in Fiji—its habits with regard to other larvae may be neglected.

To ascertain the position on the host chosen by *Ptychomyia* for oviposition a long series of parasitised *Levuana* larvae was examined from material used in breeding cages. The position on a hundred of these larvae of 152 eggs was noted, and is expressed diagrammatically (Fig. 99). The figure outlines in squares the segments of a caterpillar, each segment being separated from the preceding and successive one by a narrower space, the intersegmental crease; the latter is, of course, disproportionate in the diagram, being enlarged to allow of the marking in of eggs. The vertical lines divide the figure into a central dorsal area, on either side of which is a lateral area. The distinction between dorsal and lateral being taken for convenience as a line running through the dorso-lateral pigment spots.

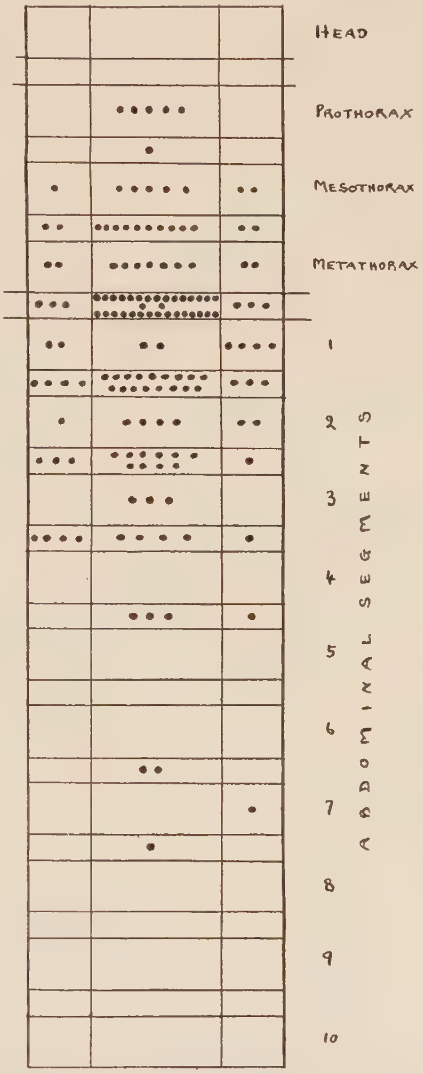

FIG. 99.—Diagrammatic representation of the external divisions of a *Levuana* caterpillar, showing the distribution of eggs of *Ptychomyia remota*. For explanation see text.

Each ink spot indicates a *Ptychomyia* egg laid in the position indicated.

This shows clearly that:

(*a*) There is a concentration of eggs in the anterior half of the host.
(*b*) Approximately 70 per cent. are laid dorsally.
(*c*) Approximately 70 per cent. are laid intersegmentally.
(*d*) No eggs are laid on the head, since it is nearly always retracted beneath the prothorax.
(*e*) No eggs are laid ventrally.

Examination of material from the field bears out the results expressed above.

6. *Stage of Host Selected.*—It is a somewhat difficult matter to get absolutely true statistics of this from field collections where larvae are present in all stages, since a percentage of the parasitised larvae disappears and that percentage tends to be higher the smaller the larva—owing to a pathological condition resulting from the relatively large wound caused by the entry of a newly hatched maggot. One has to rely, therefore, on general observations, coupled with detailed studies of the behaviour of the maggots during their growth in various stages of larvae.

Except for the fact that motionless larvae are shunned, the main factor that seems to govern the selection of a suitable host is its size.

First and second stage *Levuana* larvae are apparently too small to attract the flies ; they were offered to a female, eager to oviposit, in captivity, but were refused.

Cases of second-stage larvae with eggs have very occasionally been met with in the field, but in no cases have such larvae survived the effects of the maggot's entry, and it is therefore clear that such minute larvae are not normally suited for oviposition by the fly.

Third-stage larvae may (shortly before the third moult) be quite large enough to attract the fly, and they are freely attacked—*where larger larvae are not available.* If they are large enough to survive the effects of the entrance of the maggot, they are either killed at the next moult, in which case the issuing fly is too small to be an efficient reproductive agent, or else they continue to develop in the usual way with the maggot remaining in the first instar, until they reach the fourth or even prepupal moult, when the maggot suddenly develops rapidly and kills its host. This latter condition, however, demands the protraction of the first larval stage of the parasite to a period (in one case no less than eighteen days) far in excess of what may be supposed to be typical ; and for this reason it is supposed that oviposition on third-stage *Levuana* is not normal, but is the result of a shortage of the more suitable larger-size larvae.

Bearing in mind that they cannot be claimed (for the reason stated above) to represent the exact proportions of the stages attacked, the following statistics, obtained from collecting every larva and egg on a certain tree on a certain day, may prove of interest.

	Healthy.	Parasitised.
Fifth-stage *Levuana* . .	8	117 (93·6 per cent.)
Fourth-stage ,, . . .	9	28 (75 per cent.)
Third-stage ,, . . .	many	4 (10 per cent.)
Second-stage ,, . . .	120	1 (1 per cent.)
First-stage ,, . . .	262	0 (0 per cent.)
Eggs . . .	399	

This shows quite clearly that provided that all stages of *Levuana* are present at the same time, the flies select the fourth and fifth instar larvae for oviposition ; and this is borne out by the normal rate of development of a maggot inside a large larva, and also by very numerous observations in the field.

7. *Frequency of Oviposition on a Single Host.*—There seems to be little in the behaviour of flies in captivity to suggest that they are much influenced in their choice of a host by the presence of other eggs on it. Therefore when the supply of suitable host larvae is increased, the number of eggs laid on each larva is decreased, as one would expect. The movement of a larva is a much more active stimulus for the fly to oviposit than is the absence of other eggs on a motionless larva. Except where the supply of hosts falls far short of the demand, flies lay the majority of their eggs at the rate of one per host. This is, of course, the most economical, since only one fly can ever develop

from one host larva, no matter how many are laid on it (see paragraph on Superparasitism on p. 205).

But in the field the condition is often reached wherein flies are ready to oviposit at a time when there are insufficient large host larvae available. In such cases there are four courses open to the flies. They may either :

(*a*) Fly away and " seek new pastures " ; or
(*b*) Remain in the same place and not lay eggs until younger larvae have grown up to a suitable size ; or
(*c*) Lay all their eggs on the few available large larvae and waste many of them ; or
(*d*) Attack smaller larvae.

All these things probably happen, but (*c*) appears to be the one most freely adopted.

Under exceptional conditions a very large number of eggs (72) may be laid on one larva (see Gater, 1926), but it is seldom that more than ten are found on a single larva.

In captivity (glass jar) a single fly attacked larvae during seven days and laid its eggs as follows :—

19 larvae with 1 egg.
7 ,, ,, 2 eggs.
1 larva ,, 3 ,,
2 larvae ,, 4 ,,
2 ,, ,, 5 ,,
1 larva ,, 7 ,,
1 ,, ,, 8 ,,

whereas in a large breeding cage with ample host material available only seven out of 142 larvae parasitised had more than one egg.

Thus, as the cause of laying more than one egg on each host seems to be determined more by the available supply of the latter than by any selection habit of the fly, no useful purpose can be gained by quoting any further statistics on this subject.

8. *An Active Host Larva Preferred.*—It has been observed repeatedly in experiments conducted with *Ptychomyia* that females seem especially attracted to oviposit on a host which displays active movement.

In the case of *Levuana* the reason for this seems fairly obvious. The larvae are covered with clusters of stout bristles which form an almost impenetrable barrier round the general surface of the body dorsally and laterally, whilst the larva is at rest. As soon as it starts to crawl, the intersegmental areas become successively exposed, and it is the habit of *Ptychomyia* to follow a crawling larva until it can dart at such an exposed area and oviposit on the skin between the bristles. It has been observed that about 70 per cent. of the eggs are laid intersegmentally. This habit of *Ptychomyia* seems hardly the result of adaptation so far as *Levuana* is concerned, because eggs are occasionally laid on the bristles themselves, and in no such observed case has the hatching maggot failed to gain access to its host. Moreover, in one instance, an egg was successfully transferred with a needle from one larva, which had had two laid on it, to another larva unparasitised. The egg was in this instance merely supported by the bristles, and very loosely attached; it hatched, however, and the maggot succeeded in boring in.

Perhaps, therefore, the anxiety of *Ptychomyia* to oviposit right against the skin of the host is to avoid the risk of any eggs being brushed off, which might happen were they merely loosely attached to the bristles. Some caterpillars, *e.g. Rhesala* sp. which have been subjected to the attacks of *Ptychomyia*, have been seen to detach the eggs with their mouth parts, although this does not seem to be the case with *Levuana* where the head of the larva is retracted beneath a hood formed by the prothorax.

There is, however, another aspect to this question. For some thirty-six hours previous to each larval moult, *Levuana* adopts a contracted attitude, during which time it is perfectly motionless until the ecdysis has occurred. Were *Ptychomyia* to oviposit on such motionless larvae, as it occasionally does, the eggs would be moulted off previous to hatching when the larva casts its skin. Perhaps, then, this gives a more likely reason from the point of view of adaptation to account for the selection of crawling larvae by the female *Ptychomyia* about to oviposit.

The exact significance of the following habit is not understood, but it has frequently been observed that the female *Ptychomyia* "pats" a prospective host larva with one of its forelegs. This seems only to take place when the larva in question is more or less motionless. Whether this is to prompt the larva to renewed crawlings is not known; but in the majority of cases observed, the larva has remained completely motionless while it is being patted, and the fly has forthwith abandoned it as an object on which to oviposit.

An interesting corollary of this is the fact that if a rapidly crawling *Levuana* larva be very gently tickled with the hairs of a fine brush, it will often stop crawling and remain motionless for as long as the tickling continues, and for some ten to fifteen seconds after it has ceased.

9. *Infertile Eggs.*—One female fly kept in a glass jar with a male laid altogether sixty-nine eggs, of which eleven were infertile. The first egg laid by the fly was infertile, but the majority of such eggs were laid during the last two days of its life.

Only five infertile eggs were obtained from four female flies kept with males in a glass jar and fed with diluted honey, the total eggs laid being 125 during a period of ten days. In this case only three of the females mated (under observation) at the usual time, viz. within two hours of emergence, and it is possible that the fourth female never mated at all, and that the infertile eggs which appeared *at intervals* during the period of oviposition were all laid by this one female. Under such conditions of life the number of infertile eggs laid is less than 10 per cent.

Flies were kept in a large (6-in. by 5-in.) breeding cage, and fed with diluted honey daily. They were not confined more than this at any stage of their life. With some twelve flies in the cage, during a period of seven days, 142 eggs were laid. Of these eggs nearly 60 per cent. were infertile : the reason being that during the first few days of the period there were only two males (one too small to copulate) to ten females. After the emergence of more males, it was found that very few infertile eggs were obtained. This shows that unmated flies will lay eggs if provoked by the movements of a caterpillar.

With collections of parasitised larvae from the field the percentage of eggs which failed to hatch after the second day was only four.

Thus the normal infertility rate is probably rarely more than about 5 per cent.

10. *Egg Capacity.*—One female fly kept in a glass jar and fed daily with diluted honey laid sixty-nine eggs before she died. A post-mortem examination of her reproductive organs showed that there were no more eggs in the ovary. This, then, is a record of an absolute egg capacity of sixty-nine in a fly which had access to a constant supply of food.

Four females kept in conditions similar to the above laid a total of 125 eggs before the last female died. As the last twenty eggs were laid when only two females remained in the jar, the average per female can be estimated at thirty-five eggs. It is quite possible that one female never laid any eggs at all.

These are the only records we have made of the egg capacity.

Larvae.—(1) *Feeding and Respiration.*—*Ptychomyia remota* deposits its rather large eggs on the skin of the host ; and, until they reach the third stage, the maggots feed entirely on the fluids in the body cavity of the host (Figs. 100 and 101). They maintain connection with the outside air for respiratory purposes by means of a thickly chitinised "funnel," which is a pathological growth of host integument in response to the irritation set up by the parasite (Figs. 102 and 103). The structure and formation of this funnel, which is hypodermal in origin, is essentially similar to that described by Tothill for *Ernestia ampelus*, Walk.* With the exception that in *E. ampelus* the eggs are not laid on the host, the habits of its immature stages up to the time of emergence from the host are remarkably like those of *Ptychomyia*.

The anteriorly directed spines on the caudal segment of *P. remota* presumably prevent the larva from falling into the fluids of the host, as in *Ernestia*.

It is not certain at what exact stage the anus becomes functional. It is certainly visible in the second-stage larva, but appears to have no lumen. It is functional in the third stage ; but is probably not so before the second moult.

Moulted skins, as in *Ernestia*, are worked off posteriorly and become pressed up against the inside of the funnel of the host.

Finally, the respiratory mechanism is very similar in the two species concerned, the anterior spiracles being functionless until after the second moult.

(2) *Weak Mouth Parts of First-stage Larva.*—The boring powers of the newly hatched larva of *P. remota* are, however, rather limited. On *Levuana* it is unable to bore through the thickened integument of the pronotum, and when eggs are laid in that position, the small parasite larvae migrate to a place where the integument is softer. On caterpillars of several other

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* *The Natural Control of the Fall Webworm in Canada*, pp. 56 *et sq.*

species the parasite larvae seem unable to penetrate the skin of the would-be host. This is usually the case with caterpillars (*Rhesala* sp.) which occur in large numbers on the common strandline plant, *Tournefortea argentea.* *Ptychomyia* frequently oviposits on these larvae,* and in only one instance

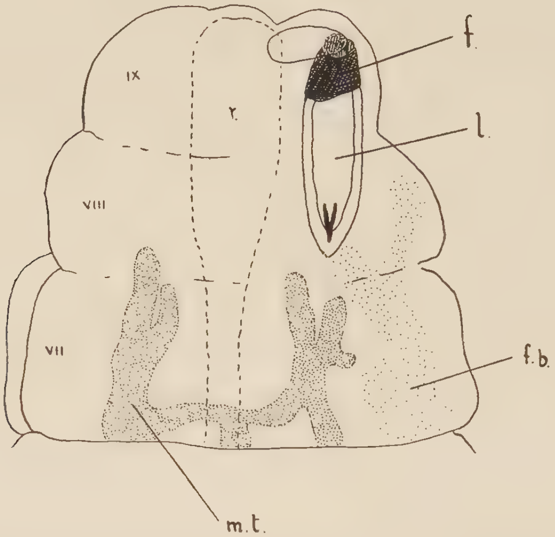

Fig. 100.—*Ptychomyia remota.*—First-stage maggot (*l.*) in body cavity of fifth-instar larva of *Levuana.* Diagrammatic. Setae omitted. *r.*, rectum of host; *m.t.*, malpighian tubule; *f.b.*, fat body; *f.*, integumental funnel; *l.*, first-stage maggot suspended inside funnel. VII, VIII, IX, abdominal segments of host.

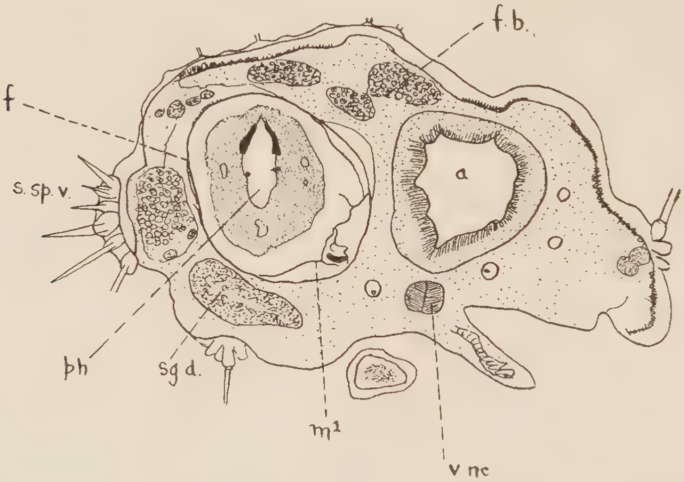

Fig. 101.—Transverse section through the mesothorax of a fifth-stage *Levuana* larva parasitised by *Ptychomyia remota.* *f.*, integumental funnel round parasite: this is through the inner part of the funnel not very thickly chitinised; *ph.*, pharyngeal cavity of second-stage *P. remota* maggot. The black areas are the pharyngeal sclerites in section; *m*^{1}., first-stage *P. remota* moult skin pushed up against the inside of the funnel. Part of the first-stage mouth parts can be seen in the centre of the skin; *a.*, alimentary canal of host; *f.b.*, fat body of host; *v.nc.*, ventral nerve cord of host; *sg.d.*, duct of silk gland (displaced ventrally by parasite); *s.sp.v.*, supraspiracular verruca.

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* Eggs were found on seven out of 150 caterpillars examined at Makuluva in January 1928.

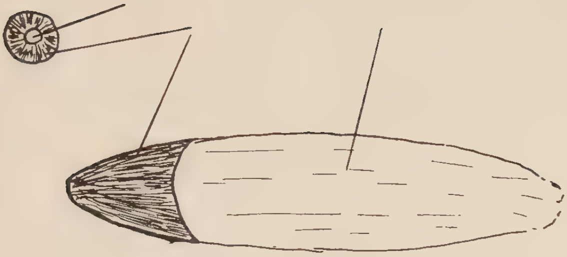

FIG. 102.—Diagram of integumental funnel of *Ptychomyia* with the larva removed. The basal funnel is chitinised. The larva maintains contact with the air through this funnel by means of two spiracles.

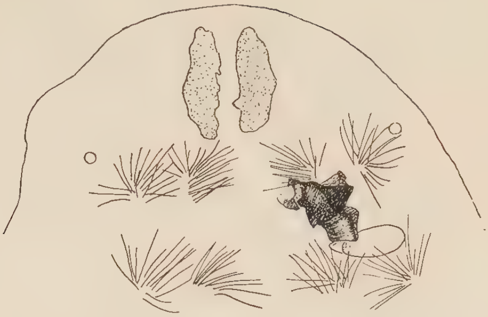

FIG. 103.—Dorsal view of thorax of prepupal *Levuana iridescens*, showing egg (hatched) and integumental funnel of *P. remota*. (This was drawn from a specimen treated with KOH and mounted in balsam.) Some of the setae of the host omitted. The two small circles on the host are the prothoracic spiracles.

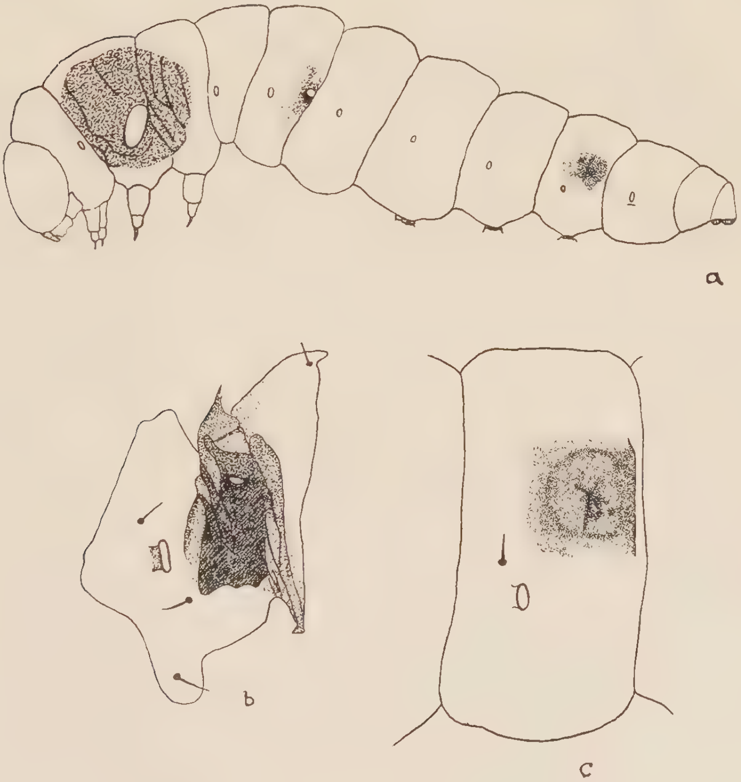

FIG. 104.—*Eublemma* sp. attacked by *P. remota*. *a.*, prepupal host larva showing local development of black and hardened integument under egg of parasite and around funnel of maggot in membrane between abdominal segments 2 and 3. And preventing the maggot's entrance in the sixth abdominal segment, × 10. *b.*, enlarged view of parasite entrance hole, × 40; *c.*, enlarged view of place in sixth abdominal segment where maggot attempted to gnaw through the integument, × 40.

did the hatching maggot manage to bore into the caterpillar.* In this case the maggot died in its first stage inside the caterpillar, which continued to develop normally. Similar cases were noted with larvae of *Terias hecabe*.†

(3) *Defence of* Eublemma *against Attack*.—Larvae of *Eublemma*, which is a true host, seem to react in a remarkable way to the attacks of *Ptychomyia*. After they have been "stung" by a fly, the integument appears to be irritated locally, with the result that an area immediately underlying the egg becomes hardened and quite black. When the egg hatches, the maggot is unable to bore through this hardened tissue and crawls to another place on the host to attempt to gain entry. Such an occurrence is illustrated by the *Eublemma* larva shown in Fig. 104. An egg of *P. remota* was laid on the mesothorax of this larva ("*a*"), the egg showing in the figure as a white object in the centre of the patch of blackened host integument. In this instance, the hatching of the egg was observed, and the maggot, after abandoning attempts to bore into the mesothorax, was seen to crawl along the side of the host's body as far as the sixth abdominal segment, where it made renewed efforts to bore in. This last effort also resulted in failure, but before discoloration of the host's integument had started. Probably the integument at this point was too thick for the tiny mouth parts of the maggot. Discoloration did eventually take place on this spot, as is shown in the figure at "*a*" and "*c*." The maggot, however, still persevered in its pursuit of nutriment, and by settling on the thin integument between the second and

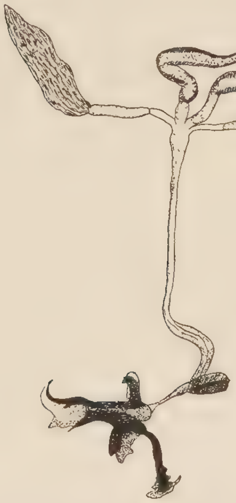

FIG. 105.—*Ptychomyia remota*.—♂ reproductive system. × 100.

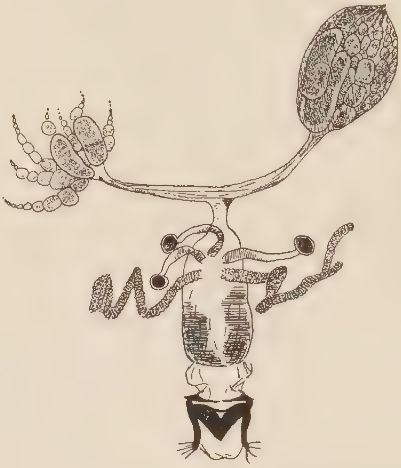

FIG. 106.—*P. remota*.—Reproductive system of ♀. One ovary dissected to show the individual eggs. × 75.

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* Some of the parasite eggs were dislodged by the mouth parts of the larva.

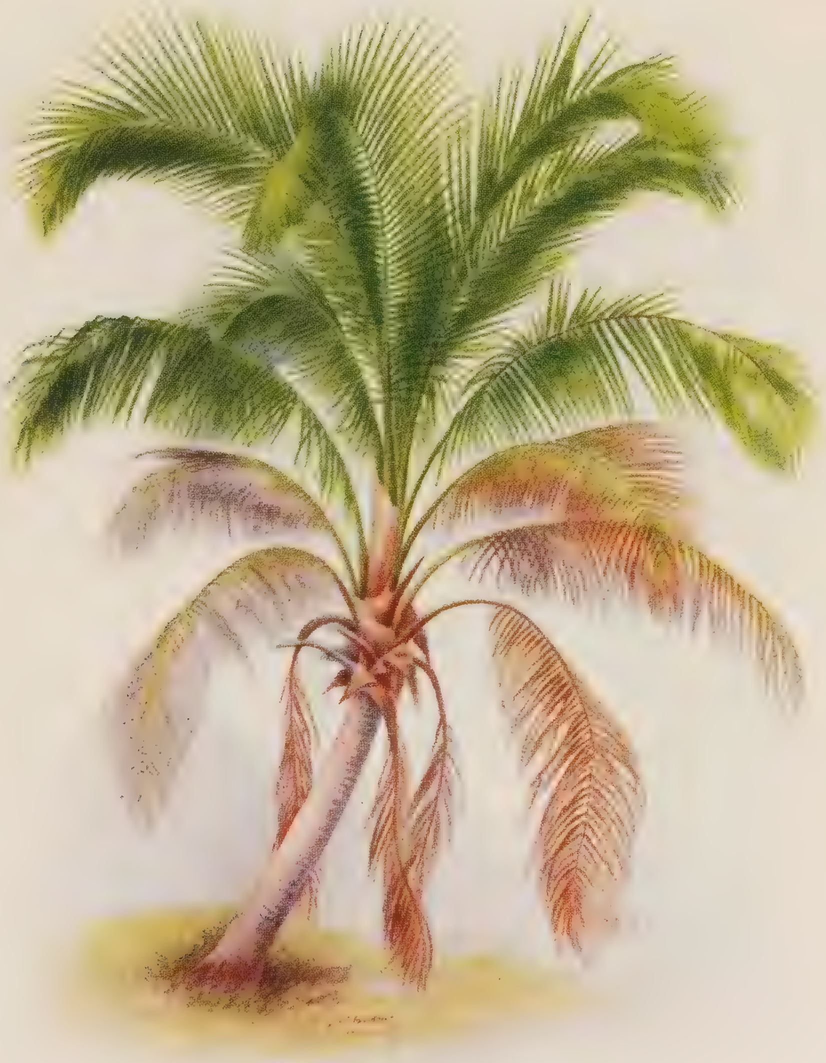
† We have two empty pupal skins of *T. hecabe*, from which adult butterflies emerged in spite of the fact that their larvae were attacked by *P. remota*, whose maggots gained partial entry to the host and then died. The incipient breathing funnel of the parasite can be seen in the pupal skin.

PLATE VII

THE EFFECT OF INTRODUCING *PTYCHOMYIA REMOTA*

The abrupt change from grey to green is due to the arrival of *Ptychomyia*. One of the periodical outbreaks of *Levuana* was reaching its peak when the fly was colonised. The parasite multiplied with great rapidity, and the parasitism reached 80 per cent. and on some trees 90 per cent. The few remaining *Levuana* were in turn annihilated at a slightly later stage by the parasite or by predators, and the tree recovered completely. Such was the history of the majority of young trees at Masese and at most places throughout the *Levuana* area.

PLATE VII



third abdominal segments managed to bore in and completed its development without further mishap. The final entrance hole of the maggot and the later developed host's "funnel" (dissected out after emergence of the parasite) are shown in the figure at "*a*" and "*b*" respectively.

This is such an interesting reaction on the part of a caterpillar to attacks by a parasite, that it is unfortunate that scarcity of material prevented a more complete investigation of the phenomenon being made; the exact stimulus which causes the discoloration of the host's integument is not known.

The case above quoted is not an exceptional one, because in each one of eleven parasitised *Eublemma* larvae collected during November 1926 there was a certain amount of discoloured host tissue round the parasite egg, and in only six cases did the larva of the latter manage to gain entry into the host.

This action on the part of *Eublemma* larvae is apparently responsible for counteracting possibly 50 per cent. of the attacks made on them by *Ptychomyia remota*.

(4) *The Destructive Feeding Stage.*—After the second larval moult, the parasite maggot enters its destructive feeding period (Tothill, *loc. cit.*), and consumes all the internal organs of its host.* The carcase of the latter becomes very distorted by the writhings of the contained maggot. The latter, when ready to pupate, either makes its exit from the skin of the host, leaving a large round hole, or else it pupates within the skin of the host, which then generally cracks slightly owing to pressure by the puparium within. There is, therefore, no difficulty in determining presence of a puparium within a host caterpillar.

(5) *Pupation and Emergence of the Adult.*—When a maggot emerges from the host, pupation usually takes place immediately, the puparium being formed beneath the cocoon of the host. Only very occasionally do maggots crawl to a distance to pupate, and they never go into the soil.

Emergence of the adult usually takes place in the morning, although exceptions to this are fairly numerous.

Although the vestiture of macrochaetae on the adult has not got the all-important part to play that it has with species that pupate underground, yet it is a significant fact that flies are able to force their way through a mass of *Levuana* cocoons, whereas the moths themselves are quite ill-adapted for such an exigency and almost invariably die.

SUPERPARASITISM

It is convenient to discuss this phenomenon under the following headings:—

1. Effect on the host:
    - (*a*) By external damage.
    - (*b*) By internal damage.

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* In the case of exceptionally large hosts, *e.g. Sylepta derogata*, only part of the host is destroyed by the maggot.

2. Effect on the parasite.
    - (*a*) Alteration of time taken for the early stages.
    - (*b*) Factors that determine which maggot reaches maturity.
    - (*c*) Methods of destroying the supernumerary maggots.
    - (*d*) Effect on the food supply.
3. Occurrence in the field.
4. Effect on the issuing brood of flies.

1. (*a*) The amount of damage done to the host by the boring in of the parasite larvae is directly proportional to the size of the host larva and the number of maggots that bore in.

Two, three, or even as many as six maggots may bore into a healthy fourth or fifth stage host without causing any vital damage to it. But on the occasions where their entrance holes are very close together it frequently happens that one or more of the funnels are ruptured by the mouth parts of another maggot, and this causes the blood of the host to ooze up through the hole, resulting in a pathological condition of the host, a cessation of feeding and ultimate death.

But the boring in of more than one maggot into a small (first, second or third stage) host larva almost always causes some vital injury to the host. In such cases the parasites may continue to feed for a day after the host dies, after which they will themselves die also.

(*b*) The internal damage to the host is also very largely dependent on the relative position of the parasites within it as far as the early stages are concerned. If all the maggots manage to survive until they are second stage, the host will also remain alive, and not until the first maggot moulting for the second time reaches its destructive feeding period will death occur to the host, in the same way as when there is only a single parasite present. In a few cases also when the successful maggot kills off the unsuccessful maggots while still first stage, the bleeding at the funnel, described above, does not proceed rapidly enough to kill the host. There is no evidence that any toxic substance is secreted by the parasites either before or after boring into the host, and it is, moreover, of vital importance to the welfare of the parasites that the host should remain alive until one of them has completed its second moult.

2. In the table dealing with superparasitised larvae (p. 192), are set forth the records of the development of maggots within twenty, fourth and fifth stage *Levuana* larvae. The latter are numbered one to twenty in the left-hand column, and each parasite is indexed *a*, *b*, *c*, etc., for each host. They are arranged in order according to the stage of host attacked and the stage at which the latter is subsequently killed, and precedence is given to those

cases where the maggots completed their development without being destroyed by a dissection of the host; furthermore, for each host precedence is given to the successful parasite. For other details about this table, consult the accompanying legend.

(*a*) In the table on p. 193 is given a comparison of the range of and mean periods for the various early stages derived from hosts with one parasite and two or more parasites. In the right-hand column it will be noticed that there is only a very slight difference in the length of parasite larval development in either normally or superparasitised hosts. Any difference there may be would be accounted for by the occasional death of the host slightly prior to the second moult of the primary parasite, causing an abbreviation of the third stage of those maggots which are accompanied by others in the same host.

It was found that in the twenty host larvae used experimentally the incubation period of five (Nos. 1, 12, 16, 18 and 20) of the successful maggots was shorter than that of the unsuccessful maggots in each respective host, whereas in eleven cases (Nos. 2, 3, 5, 7, 9, 10, 11, 13, 14, 15 and 17) the incubation period was of equal duration; but four (Nos. 4, 6, 8 and 19) had actually a longer incubation period than those which they subsequently killed, so that the first maggot to enter the host is not always the one that ultimately matures. The mean period for the incubation and first stage together of the two classes of maggots was slightly (less than twelve hours) longer for the unsuccessful maggots than for their respective successful competitors. This is in accordance with expectation, since it is the combined length of these two stages in development which determines the fate of the parasites; for in every case observed the maggot which reaches the second stage first is the one that dominates, except in cases of a "dead heat" to first moult, when brevity of the second stage decides between the competitors.

The object of referring to this here is, however, to show that the successful maggots do not exert any appreciable retarding influence on the rate of development of the unsuccessful maggots, nor do the latter accelerate the development of the former. Every parasite in a superparasitised host behaves exactly the same way as if it were alone in a host until such time as it actually comes in contact with another maggot in its search for food.

(*b*) It has already been pointed out that no toxic substance is secreted by a maggot to prevent the feeding of another maggot in the same host, and also that the first egg to hatch does not necessarily produce the successful maggot. The real cause of one maggot being able to assume a dominant position is determined by the rate of development after the first moult has taken place, for whereas deaths due to the close approximation of maggots in the same host are of frequent occurrence in the first stage, it often happens (*e.g.* in 13/20 of all the cases we record) that more maggots than one undergo their first moult at approximately the same time; in such cases the second stage maggots will continue to develop unimpeded, provided that they do not meet each other; for should this happen one will kill the other by rupturing its funnel and causing it to drown in the blood of the host. If, however, they do not meet and continue to feed, the one which completes the second moult first will become the dominant maggot, because during the third stage the maggot leaves its breathing funnel, and in a period of little more than a day eats everything inside the skin of the host, including any other parasite larvae. In no single case observed in Fiji was more than one third-stage maggot discovered inside the same host—although Gater has reported one case of this occurring in Malaya.

(*c*) During the first and second stages of the primary maggots there is little difficulty in securing an adequate supply of food should the host be in a healthy condition and not overcrowded by unsuccessful maggots. Thus any maggots which are killed before the successful one reaches third stage are not eaten but remain dead inside their ruptured funnels.

In all dissections it was found that no damage had been done to such larvae—death resulting presumably from drowning caused by the blood of the host oozing through the punctured breathing funnel. Such funnels may often be readily distinguished without dissection, because the blood contained in them may work out and form a drop on the surface of the host, or if not that it will at any rate obscure any view of the spiracles of the contained maggot.

But when the successful maggot has reached third stage and starts its destructive feeding, any other maggots, whether dead or alive, will be readily eaten, nothing remaining but their mouth sclerites and integumental funnels.

(*d*) It might be thought that the presence of a large number of maggots in the same hosts would so exhaust the food supply that the maggot which reaches maturity would be much under size. But, as pointed out above, the successful maggot not only consumes the balance of the host tissues but also feeds on the bodies of its less fortunate comrades. In this way the maggot which issues from a much superparasitised host is not abnormally small. The size of puparia and adults is directly dependent on the size of the host when the destructive feeding stage is reached, and there is much variety in this respect.

3. The occurrence of superparasitism in the field is general: its intensity is, however, governed by the ratio between adult parasites and suitable

hosts in any one instance. Flies have not the slightest compunction in ovipositing on larvae which are already well stocked with parasite eggs, and if the supply of suitably aged larvae is limited, the percentage of them on which are laid more than one egg is very high.

During the first six months after *P. remota* was liberated in Fiji, *Levuana* was in such large numbers and in all stages at once that the percentage of superparasitised larvae seldom exceeded 20 per cent. in any locality where the fly and moth were abundant. But during the latter half of 1926 and in 1927 a control of the host was reached; and *Levuana* not only became comparatively rare, but got into that condition where only certain stages of the life-cycle were present at any one time in the same locality. Under these circumstances the precentage of superparasitised larvae increased considerably on occasions, and in a count made recently on Makuluva, at a time when the total parasitism was less than 10 per cent., no less than 65 per cent. of the parasitised larvae examined had more than one egg laid on them.

4. Because the presence of other maggots in the same host has no effect on the issuance of the parasite, the waste through superparasitism has no great detrimental effect on the strength of the issuing generation of parasites when the balance between the percentage of superparasitism and prevalence of the host is considered. Furthermore the fly cannot be accused of being loath to leave a locality, where the host supply of the right stage is limited, and seek new country, since its powers of diffusion have on several occasions been proved to be remarkable.

It is interesting that when we first bred *P. remota* in Fiji during August and September 1925, we started by isolating host larvae with more than one parasite egg. All superparasitised hosts were placed into a separate breeding cage, which gave an issuance of 81 per cent. adult flies as compared with an average issuance of 60 per cent. for several other cages containing only host larvae with a single parasite egg.

This shows that a moderate (perhaps 20 per cent.) proportion of eggs laid in the field are moulted off or fail to hatch, and that the waste from superparasitised hosts is probably little more than from an equal number of eggs laid each on a separate host.

5. To sum up, it may be said of superparasitism that its effects both on the development of the maggot and the strength of the succeeding generation of parasites are remarkably slight; and it would hardly be appropriate to discuss it in such comparative detail were it not such a very general phenomenon in the field and for that reason a matter worthy of full investigation.

ALLIED ZYGAENIDS AND SOME NOTES ON THEIR NATURAL CONTROL

Allied Zygaenids in other countries have played a very important part in the *Levuana* Campaign. The following is a list of species (with the countries in which they are native) which have been useful either for yielding parasites or as indications of the natural habitat of *Levuana* :—

1. *Artona catoxantha*, Hamps., in Malaya and Java.
2. ,, *trisignata*, Snell., in Java.
3. ,, *albicilia*, Hamps., in Java.
4. Zygaenid F (*Artona* sp.) in Java.
5. ,, B in New Britain.
6. ,, C in New Guinea.
7. ,, D in New Guinea.
8. ,, X (*Artona* sp.) in the Solomons.
9. ,, Y in the Solomons.

Of these, Zygaenids F and X have not yet been determined, and B, C, D, and Y are only known in their early stages.

The investigations which have been made in Malaya, Java, and the New Guinea region of Zygaenids allied to *Levuana* were conducted primarily for the purpose of discovering parasites and predators which might be suitable for controlling *Levuana*, and of devising methods for their importation into Fiji if they should be required. A study of the life-histories of some of their hosts was a necessary part of the work in so far as it concerned the breeding of those hosts on board ship to provide food for parasites. As regards the parasites themselves, it was necessary to pay special attention rather to the methods of breeding them on a large scale in captivity than to the various details of their development, and therefore the observations are very incomplete in many cases.

In the account which follows of certain Zygaenids allied to *Levuana* all the more important parasites are recorded and their habits are briefly described. The four natural enemies which have been imported into Fiji are described in greater detail on pp. 16–34.

1. ARTONA CATOXANTHA, Hamps. (Plate XXXI, Fig. 2)

Systematic

1. Hampson, *Faun. Ind. Moths*, I, 1892, p. 233.
2. Jordan, *Seitz. Macrolepidoptera of the World*, X, p. 44.

Range

Malaya, Sumatra, Java, Borneo, Labuan, and Tenasserim.

Food-plants

Cocos, *Metroxylon*, *Areca*, *Arenga*, *Phoenix*, *Oncosperma*, *Calamus*, *Nipa*, *Oreodoxa*, and probably several other palms. Occasionally larvae are found feeding on *Musa*, but these have probably dropped from overhanging coconut palms.

A. catoxantha is well-known in Java and Malaya as a pest of coconuts.

Life-history

A. catoxantha and its control have been studied in great detail in Java by Leefmans.* The life-history in Malaya has been outlined by Gater, who has also discussed the more important controlling factors. It will therefore suffice here to give a brief account of this insect and its chief parasites for comparison with *Levuana*.

Egg.—The eggs are laid in small, very irregular, batches on the underside of the leaflets, and usually in the distal halves of the latter. The surface of the egg is very finely reticulated in the same manner as all the other species of *Artona* examined.

The average incubation period is one and a half days.

Larva.—The newly-hatched larva is pale green and translucent. It begins feeding a few hours after leaving the egg. The method of feeding is identical with that of *Levuana*, the lower epidermis of the leaf being stripped in straight lines between adjacent veins of the leaf.

There are five larval instars. In the third instar the colours and markings of the mature larva begin to appear. In the last instar the larva often feeds at the edge of the leaf, eating away the upper epidermis as well as the lower, and in this respect it differs from *Levuana*.

In general appearance, the full-grown larva is of a pale greenish-yellow colour, with a dark brownish-blue stripe down the middle of the back. The first two thoracic segments are yellow and without markings. The dark mid-dorsal stripe extends from segments 3 to 12. An irregular blotch of the same colour is present on either side of segments 3, 4 and 11. There are three longitudinal rows of tubercles on either side, two sub-dorsal and one lateral, extending from segments 2 to 12. Each row is represented by one tubercle on each of these segments. There are no tubercles on the prothoracic segment. All the tubercles bear many bristles. Those on the first sub-dorsal row of tubercles are all of nearly the same medium length ; the second sub-dorsal tubercles bear one long bristle and many shorter ones ; and the lateral tubercles bear bristles of various lengths, but do not possess

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* A complete account of this work is expected shortly.

one specially long one. The first thoracic segment forms a hood over the head.

The total duration of the larval stage is about three weeks.

Cocoon.—The whitish cocoon, unlike that of *Levuana*, is formed on the undersides of the leaves. In shape, form, and texture it is identical with that of *Levuana*, but is rather larger as a rule. The method of formation of the cocoon by the larva was found to be exactly the same as that described for *Levuana*.

The prepupal period, which is passed in the cocoon, occupies about two days.

Pupa.—The pupa is yellow and translucent, becoming darker and more opaque as development proceeds. It is of the typical Zygaenid form. It bears a number of spines whose number and distribution varies according to the sex. The male pupa bears on the dorsal plate of each of the abdominal segments from 3 to 8 inclusive a transverse band of numerous short, sharp, chitinous spines or teeth, situated nearer the anterior edge of the segment than the posterior. The teeth are very irregularly arranged and are not in a single row. The cremaster on the terminal segment is represented by twenty to twenty-five spines which are hooked at their extremities. The spines and teeth are directed backwards.

The female pupa differs from the male in several respects. There is a transverse row of chitinous teeth on segments 3 to 7 only, and the teeth are arranged in a single row on each segment. Moreover, each tooth arises from an elongated, rectangular, strongly-chitinised plate, which is much larger than the tooth, and all the plates on each segment are arranged side by side and close together. These plates are never developed in the male. Occasionally a few teeth are present on segment 8. In addition to the teeth on each of the segments from 3 to 7 there are small groups of straight spines, one group on either side of the middle line. Each group contains from four to ten spines and is situated behind the row of teeth. The spines are also present on segments 2 and 8. The cremaster consists of a number of hooked spines as in the male, but there are always more in the female (usually thirty to forty). The teeth and spines are important specific characters.

The duration of the pupal stage (including the prepupal) is eight days.

Adult.—When the moth is ready to emerge, the pupa thrusts itself halfway out of the cocoon. Copulation occurs on the same day as emergence, and oviposition begins on the following day. The moths will not feed or oviposit in small receptacles, such as glass jars, but will do so readily in suitable large cages. We obtained most satisfactory results by enclosing the moths in large wooden cages (6 ft. high) with cloth windows on two sides and a glass window at one end. Young growing palms were placed in each cage, in contact with the glass, and the leaves were sprinkled with dilute sugar solution. The moths fed, copulated, and oviposited readily in these cages. At least one glass window is essential, and the cage must obtain the maximum possible light without being in the full sun. Both sexes fly by day.

The Life Cycle may be summarised as follows :—

Incubation of egg		4½	days.
Larval Stage		22	,,
Pupal Stage		8	,,
Emergence to Oviposition	about	2	,,
Total		36½	,,

These are approximate means. Actually the duration of the life-cycle from egg to egg varies from thirty-three to thirty-eight days or even more.

Occurrence of Outbreaks and Nature of Damage

Serious damage is occasionally done to coconuts in Malaya and Java by this pest, but the damage is never so serious as that caused by *Levuana* prior to the importation of parasites. Outbreaks are comparatively few and far between. They never begin during the wet season. They are, moreover, always controlled by natural enemies. The control by this means is slow on account of the presence of an abundance of secondary parasites, but in many cases the advent of the wet season in the later stages of an outbreak accelerates the suppression of the pest. Outbreaks are always controlled before the available food-supply is exhausted, but not before considerable damage is done to the trees. The lower leaves of the trees are attacked and killed first, and often the control is complete before the upper leaves are attacked. Although the trees are greatly weakened and the crop of nuts greatly diminished, trees are very rarely, if ever, completely killed. Outbreaks seldom last for more than eight generations of the moths, and are usually controlled after five or six generations. There is no regular periodicity in the occurrence of outbreaks. *A. catoxantha* is often very rare in all parts of Malaya and Java, and there may be no outbreaks anywhere for a period of one or two years. It is clear, therefore, that in normal circumstances *A. catoxantha* is not a pest at all. A natural equilibrium is normally maintained between this insect and its primary and secondary parasites, and it is only when some unusual circumstance, affecting either the primaries or the secondaries, arises that the equilibrium is upset in such a manner as to permit *Artona* to multiply to an abnormal extent. What the unusual circumstance is we do not know.

Natural Enemies

A. catoxantha has many natural enemies, nearly all of which are parasites. The only common predator is the Clerid beetle, *Callimerus arcufer*, Chpn., which attacks the larvae and pupae. The primary parasites include Tachinids, Ichneumonids, Braconids, Chalcidids, and Proctotrupids. The most common of them are :

1. *Ptychomyia remota*, Ald. (Tachinid).
2. *Degeeria albiceps*, Macq. (Tachinid).
3. *Apanteles artonae*, Rohw. (Braconid).
4. *Euplectrus* sp. (Eulophid).
5. *Mesostenus* sp. (Ichneumonid).

All these occur in both Java and Malaya, but their order of importance is not the same in these two countries. In Malaya, by far the most effective as a control is *Ptychomyia remota*, and the next is *Apanteles artonae*. In Java, *Degeeria albiceps* is usually the most important, and is followed by *Apanteles artonae* and *Ptychomyia remota*.

Secondary parasites attack all these primaries commonly, and greatly diminish their efficiency. Several of the parasites that are normally primaries are sometimes secondaries also.

No egg parasite has been found in nature, but *Trichogrammatoidea nana*, Zehntner, which commonly attacks the eggs of *Artona trisignata* in Java, was found to attack those of *A. catoxantha* very readily in captivity.

1. and 2. Ptychomyia remota attacks half-grown larvae, usually those in the third instar. A detailed account of it as a parasite of *Levuana* has already been given, and this applies in nearly all respects to *A. catoxantha* also. The habits of *Degeeria albiceps* are similar. According to Gater the approximate percentage of parasitism by *P. remota* usually amounts in Malaya to 40 per cent.

3. Apanteles artonae, Rohw.*—The only known hosts of this parasite are *A. catoxantha* and *A. trisignata*, and it is recorded only from Malaya and Java. Apparently it does not occur above 2,000 ft.

It is an internal parasite, and it attacks younger larvae than the Tachinids. The host larvae are either in the first or second instar when *Apanteles artonae* oviposits in them. The presence of the parasite within the host larva retards the development of the host, but does not stop it until the parasite larva is full grown, by which time the host is nearly always in the third instar. Only one parasite results from each host larva. The duration of the egg and larval stages together is about ten days, but appears to vary from eight to twelve days. The duration of the pupal stage (including the prepupal) is four and a half to five days. The life-cycle from oviposition to emergence therefore covers approximately fifteen days.

When the parasite larva is mature within its host, the latter spins a few threads on the leaf as if it were about to moult. Soon afterwards the parasite bites a hole in the middle of the side of the host and then emerges slowly through the hole. It starts spinning its cocoon, which is formed underneath the host, before it is completely outside the host. When only the anterior end is free, it turns towards the posterior end of the host and spins a few threads from the side of the host to the leaf. These threads are the foundations of the cocoon and serve to attach the host to the leaf when the parasite pushes its way underneath, and the formation of the cocoon is always begun underneath the hind end of the host. The emergence of the parasite from the host occupies about ten minutes, and when it is entirely free, it makes its way underneath the host at the hind end of the latter, spinning continuously all the time. After four hours, the cocoon is complete and the parasite is stationary within it. Pupation does not occur until the following day.

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* (1) Rohwer, *Proc. Ent. Soc. Wash.*, xxviii, 1926, p. 188; (2) Wilkinson, *Bull. Ent. Res.*, xix, 1928, p. 92.

The cocoon is white, opaque, and tough, and is an elongate ovoid in shape, with broadly rounded ends. The remains of the host larva remain attached to it and cover it except at the sides. The adult emerges by making a circular cut, of which the two ends do not quite meet, round the end of the cocoon and then pushing this end outwards liked a hinged lid.

The adults are difficult to breed and to feed in captivity. They die within three or four days if fed on sugar solution, but if they are provided with drops of very dilute honey in water twice every day, the females can be kept alive for two weeks easily, though rarely much longer. We have, however, kept a few individuals alive for three weeks, and Mr. Leefmans in Java has succeeded in doing so for one month. It is desirable to keep them in partial darkness for at least half of each day to reduce their activity. The males always die within four or five days.

Many failures to breed this parasite are recorded, but actually it is not difficult to breed if suitable cages are made. It is useless to attempt to breed it in glass tubes, jars, or small cages. It must be provided with conditions that are as natural as possible, namely, ample room, plenty of light, and a good supply of host larvae of a suitable age. The large wooden cages (6 ft. high), with at least one glass window and the remaining windows of cloth, which were used for breeding its hosts, *Artona* spp., are most suitable for this parasite. An abundant and constant supply of host larvae is essential, the more the better, and it is the maintenance of this supply which is the chief difficulty. We found that the best way of feeding the parasites in the cages is to spray the honey solution over the uppersides of the leaves of the food-plant of the host, and also on the glass window, at least four times a day by means of an atomiser. The minute drops evaporate very quickly in large cages, and the spraying might with advantage be carried out every hour. The adults do not live so long in the cages as in glass tubes, but they will not oviposit in tubes.

There are many secondary parasites that attack *Apanteles artonae*. The most common is Chalcid C, which is not yet identified. This Chalcid is an ectoparasite of the pupae. It is capable of detecting the presence of a mature larva of *A. artonae* inside the Zygaenid larva before the former begins to emerge. Nine adults of Chalcid C were observed resting on a larva of *Artona catoxantha* from which an *Apanteles* larva was about to emerge. As the head of the *Apanteles* larva was thrust through the skin of its host the secondary parasites swarmed on to it and stung it repeatedly. Their efforts, however, did not paralyse the *Apanteles* or hinder it in any way, for it completed its cocoon in a perfectly normal manner although it was constantly stung by Chalcid C throughout the operation. The secondary parasites contrived to remain outside the cocoon, and did not lay any eggs until the cocoon was complete. The eggs are laid inside the cocoon, either on the contained *Apanteles* or on the surface of attachment of the cocoon. The duration of the egg stage is one day only, and the total duration of the life-cycle from oviposition to emergence is sixteen days. Many individuals of Chalcid C result from a single *Apanteles*. They are often so numerous that they completely cover the *Apanteles*, on which they feed externally, inside the cocoon.

4. Euplectrus sp.—This primary ectoparasite of the mature larva is often common in Java, but it certainly is not sufficiently common to play any appreciable part in the control of an outbreak of *A. catoxantha*. According to Mr. Leefmans, it is much more plentiful in localities where *Artona* is not sufficiently numerous to constitute an "outbreak."

The eggs are laid on the surface of the full-grown larva, often after the latter has made its cocoon. The resulting parasite larvae feed externally on the host, and sometimes as many as twelve mature on one host. They pupate on the surface of the remains of the host without making cocoons. The life-cycle from oviposition to emergence covers about sixteen days.

This parasite must not be confused with another species, probably of the same genus, which also occurs in Java but is much rarer. This other species is almost identical with the commoner species in habits, differing only in that its larvae pupate underneath the remains of the host instead of on its back and sides.

Euplectrus sp. is easy to keep alive in captivity and will breed well in glass tubes.

5. Mesostenus sp.—This insect, which has not yet been determined, occurs in Malaya and Java as a parasite of the pupae of *Artona catoxantha* and *A. trisignata*. It is fairly common in both countries, but is never abundant. Another known host is *Acrocercops cramerella*, Sn.

The ovipositor is thrust through the cocoon of the host during oviposition, and the egg is laid on the surface of the host pupa. The duration of the egg stage is less than two days. The larva feeds externally on the host, changing its position from time to time. There are three larval instars. Pupation takes place in a flimsy, white, elongated cocoon which is formed inside the cocoon of the host. Only one parasite matures in each host cocoon. The life-cycle from oviposition to emergence covers about eighteen days.

2. ARTONA TRISIGNATA, Snell. (Plate XXXI, Fig. 1)

Systematic

1. Snellen, *Tijdschr. Entom.*, XLV, 1902, p. 235.
2. Jordan, *Seitz. Macrolepidoptera of the World*, X, p. 44.

Range

Known only in Java, but probably occurs in Sumatra and Malaya also. Present in all parts of Java, from sea-level to 5,000 ft.

Food-plants

The larvae of this Zygaenid feed exclusively on plants of the family Zingiberaceae. The most frequently selected species are *Nicolaia* and *Hornstedtia elongata*, and all the other plants on which the larvae have been observed feeding are similar in appearance, though often not in size, to these two species. The more aberrant genera of the family, such as *Costus*, are never attacked even though they are often growing close to clumps of *Nicolaia* which are badly attacked.

The following is a list of food plants :—

1. *Nicolaia speciosa*, Horan.
2. *Nicolaia intermedia*, Val.
3. *Hornstedtia elongata*, K. Schum.
4. *Hornstedtia minor*, Val.
5. *Alpinia rhomburgiana*, Val.
6. *Alpinia hookeriana*, Val.
7. *Alpinia malaccensis*, Rose.
8. *Achasma coccineum*, Val.
9. *Achasma megalocheilos*, Griff.
10. *Zingiber macroderma*, K. Schum.
11. *Zingiber odoriferum*, Blume.
12. *Michelia champaca*, L.
13. *Amomum cardamomum*, Willd.

In spite of the variety of plants included in this list, there are several plants belonging to some of the above genera which the larvae never attack, although eggs are occasionally laid on them. In two cases at least the reason for this abstinence is that the undersides of the leaves are covered with rather long hairs which prevent the newly hatched larvae reaching the lower epidermis.

LIFE-HISTORY

The life-history was worked out in considerable detail both in the field and in the laboratory. Three successive generations, and many more separate broods, were reared under various artificial conditions in the laboratory, and the corresponding generations were studied in a bad outbreak in the field.

Egg.—The eggs are laid in batches on the undersides of the leaves of several different Zingiberaceous plants. The upper leaves are usually selected first. The number of eggs in each batch varies from ten to sixty, about thirty being the usual number. The eggs in each batch are very irregularly arranged and are not in contact with one another. The distance between adjacent eggs varies considerably, but on the average it is equal to approximately twice the diameter of one egg.

In shape the egg is almost cylindrical, and it is attached to the leaf in such a position that its long axis is almost perpendicular to the leaf. The attached end is quite flat, and the micropylar end is rounded. A longitudinal section is nearly rectangular, the opposite sides being almost parallel, but the micropylar end is slightly smaller than the base and the greatest diameter is at about a third of the length from the base. A transverse section is circular. The egg-shell is perfectly transparent and is reticulated so as to have the appearance of a very fine network composed of a fairly regular series of elongated hexagons. The greatest diameter of the egg is two-thirds of its length. It is pale green in colour, becoming slightly darker two days after oviposition ; and twenty-four hours before it hatches two dark spots (the pigment spots of the contained larva) appear faintly at the apical end and rapidly become larger and darker as development proceeds.

The incubation period was always five days at Buitenzorg, but is longer at higher altitudes. All the eggs of any one batch hatch within two hours of one another.

Larva.—The young larva breaks through the shell at the apical end. It does not eat its egg-shell, but begins feeding on the underside of the leaf in such a manner as to remove the lower epidermis in a straight line between two adjacent veins of the leaf. The young larvae are more or less gregarious and never stray far from their empty egg-shells until the second moult. A large continuous area of the lower epidermis is therefore stripped off before the second moult, and the leaf consequently has a very characteristic appearance which makes it easy to detect the young larvae.

The duration of the first instar varies from three to four days, and the duration of the second instar is three days. Up till the second moult the larva is uniformly bright green in colour, but at the second moult the colours of the mature larva appear. Three days later the third moult occurs and the larva then begins eating right through the leaf, either at the edge or in the centre, and no longer feeds in a straight line. The duration of the fourth instar is from three to four days. When only a few larvae are present on one plant, they often disperse to different leaves in the fourth instar, but in a bad outbreak the larvae from each batch of eggs remain markedly gregarious throughout their development, and in such cases they arrange themselves side by side, practically in contact with one another, and all feed at the same edge. Consequently, a large leaf of *Nicolaia* is devoured very rapidly. The larva feeds throughout its life by pressing the anterior end of the hood-like first thoracic segment against the leaf like a sucker, the head being invaginated into this segment. On one occasion two second-instar larvae were observed feeding on another larva of the same stage which had been killed by a predacious bug, but this is very unusual and the larvae are not normally cannibals.

The full-grown larva * is of a deep opaque colour. The head and first thoracic segment are black. The second thoracic and the last abdominal are uniformly red. The remainder of the body is pink dorsally and sub-dorsally, the pink area extending down the sides as far as the spiracles. There is a thin dark-red line mid-dorsally, and on each side two similar sub-dorsal lines, making five longitudinal lines in all in the pink area. The first sub-dorsal line is sometimes interrupted between the segments and is not so dark as the mid-dorsal and second sub-dorsal lines. On each segment from 2 to 12 there are two tubercles, one above the other, on either side, making in all four longitudinal rows of tubercles. The upper row on each side is situated on the first sub-dorsal line and the lower row lies between the second sub-dorsal line and the spiracles. Each tubercle bears one long bristle and many short ones. The first thoracic segment forms a hood over the head.

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* See p. 53.

The larva is mature and ready to pupate four or five days after the fourth moult.

Cocoon.—The cocoon is usually formed either on the underside of the leaf of the food-plant against the midrib, or, more rarely, on dead leaves on the ground. When a dead leaf of the food-plant still remains attached to the stem nearly all the larvae which have been feeding on that plant crowd on to the one dead leaf to pupate. In one instance sixty-seven cocoons were formed on one dead leaf, in spite of the fact that several healthy leaves still remained on the same stem, and the cocoons were so crowded that many of the resulting adults were unable to emerge.

The cocoon is almost white, greatly flattened, and elliptical in outline. It consists of a framework of closely woven silk which is impregnated with a loose, white, powdery substance, and has a tough, parchment-like texture. It is, in fact, similar in both size and appearance to the cocoons of *Levuana iridescens* and *Artona catoxantha*, and the description given elsewhere of the peculiar method of formation of the cocoon of the former applies in all respects to this species also.

Pupation takes place within the cocoon two days after it is formed.

Pupa.—The pupa is very pale green in colour and is of the typical Zygaenid form. The cuticle is soft, very thin, and transparent. The sheaths of the appendages are very long and are free for the greater part of their length. Frequently the sheaths of the proboscis and the second and third legs extend posteriorly as far as the penultimate abdominal segment. There is a transverse band of minute but strongly chitinised teeth on the dorsal plates of some of the abdominal segments (segments 3 to 8 in the male and 3 to 7 in the female). The teeth are arranged irregularly in each band, never in a single row, and each band is situated in the anterior half of each segment at about a third of the width of the segment from its anterior edge. The teeth are directed backwards. The difference in arrangement of the teeth according to sex, which is noted for *A. catoxantha*, does not occur in this species, nor are the teeth in the female mounted on chitinous plates. The cremaster on the posterior segment consists of a number of much larger spines, each of which bears a minute hook at the tip. The number of these terminal spines varies, but is always approximately twenty in both sexes.

Adult.—On the day before the adult emerges from the cocoon, the pupa assumes the adult colouring, and shortly afterwards the pupa pushes itself out from underneath one end of the cocoon so that the head and thorax are exposed. This is effected by a circular wriggling movement of the abdomen which brings the spines in contact with the inside of the cocoon. Sometimes the adult emerges immediately the pupa thrusts itself out of the cocoon, but it often waits several hours. The time that elapses between the formation of the cocoon and the emergence of the imago is from seven to nine days—usually eight days at Buitenzorg.

Copulation usually occurs on the same day as emergence. The males show great excitement when a newly emerged female is put in a cage with them, and as a rule copulation takes place about five minutes later and lasts about half an hour. Oviposition commences in the early morning of the following day. The duration of the adult life in nature is doubtful, but the males live longer than the females. In captivity the females do not live longer than four days. They feed readily on honey and water, sugar and water, or water alone. The attitude of the adult when at rest is identical with that of *Levuana*, the end of the abdomen being in contact with the leaf while the head and thorax are held well away from it. Both sexes fly by day. Fertile females will oviposit in large light cages which contain a supply of the food-plant, but they will not oviposit in glass jars. They seem to lay more readily if a large number of individuals are crowded together.

Summary of Life-cycle.—

Incubation of egg	5 days.
First instar	3 ,,
Second instar	3 ,,
Third instar	3 ,,
Fourth instar	3 ,,
Fifth instar	4 ,,
Pupal stage (formation of cocoon to emergence)	8 ,,
Emergence to oviposition	1 day.
Total	30 days.

The figure quoted for each stage represents the average period observed for that stage in the laboratory. In each brood there are always a few larvae that develop more rapidly, and a few that develop more slowly, than the majority, but these exceptional individuals were not taken into account. Thirty days is the usual period for the complete life-cycle, but it is liable to vary from twenty-eight to thirty-four days. This amount or variation was observed in the laboratory and was confirmed by observations made in the field on isolated broods. The result of it is that in a bad outbreak of this Zygaenid considerable overlapping of generations occurs after three or four broods, but the outbreaks always appear to be checked before this overlapping reaches such proportions that it is possible to find all stages present in one locality at the same time. In one case eggs and third-instar larvae were found together after six generations, but this is the greatest divergence yet observed, and the outbreak was terminated by natural enemies in the following brood.

Extent of Damage to Food-plants

The plants which this Zygaenid attacks are of little economic importance, but it is interesting to compare the nature and extent of the damage done by it with that due to its close allies *Artona catoxantha* and *Levuana iridescens* on coconuts.

The feeding habits are similar in all three species, the lower epidermis being stripped off in straight lines, and the only difference is in the ages reached by the larvae before they begin eating right through the leaf. In the present species this occurs after the third moult, in *Artona catoxantha* after the fourth moult, while in *Levuana* it does not occur at all. This difference is no doubt due chiefly to the much softer texture of the leaves of Zingiberaceae as compared with the leaves of coconuts.

The damage done by this Zygaenid to *Nicolaia* and *Hornstedtia* is often very extensive, but on other plants the larvae are rarely sufficiently numerous to do much harm. An average clump of *Nicolaia* in the forest is about 12 ft. high and consists of about five thick, straight stems each of which bears about twenty large leaves. In a bad outbreak a clump of this size may be completely destroyed after four generations of the Zygaenid. Leaves attacked by young larvae die because the greater part of the lower epidermis is removed, and those attacked by older larvae are often completely eaten away except for the midrib. There is no doubt that this Zygaenid would become quite as serious a pest as the coconut species if its food-plants were of economic value.

NATURAL ENEMIES

Outbreaks of *A. trisignata* appear always to be checked before the supply of the food-plants is exhausted. This control is effected entirely by parasites and predators. The following list of natural enemies is probably complete :—

Attacking the Egg :
  Trichogrammatoidea nana, Zehntner.
Attacking the Larva :
  A. Predators :
    (1) The nymphs of a Peptatomid bug.
    (2) A minute brown ant.
    (3) A Clerid beetle.
    (4) Chalcid B. (Adults.)
    (5) A large black ant.
    (6) A Syrphid.
  B. Parasites :
    (1) Chalcid B.
    (2) *Ptychomyia remota,* Ald.
    (3) *Apanteles artonae,* Rohw.
    (4) Chalcid D.
Attacking the Pupa :
  A. Predators :
    (1) A black ant which attacks the larva.
  B. Parasites :
    (1) *Mesostenus* sp.
    (2) Ichneumon A.

(Full-grown larvae are very frequently attacked by a Chironomid fly which sucks their juices. As many as five flies were often observed on the back of one larva. Larvae which had been bitten by this fly were collected on several occasions ; but none of them seemed to be harmed in any way and all produced adults. The Chironomid therefore cannot be classed as a predator.)

Of the eleven natural enemies mentioned above only two attack their host sufficiently frequently and regularly to make a detailed study of them worth while, from an economic point of view. These two are the egg-parasite and Chalcid B, which are dealt with separately.

Of the remainder, the black ant is the most effective, though as a predator it is too promiscuous to be of any permanent value as a control. It attacks the full-grown larvae as they begin to make their cocoons, and also the pupae, and although it is nearly always present on the plants it never attacks immature larvae. A few pupae are destroyed by it in nearly every batch, and in one case 96 per cent. of the cocoons were found to have been emptied by it, but this is unusual. It bites a small hole in one end of the cocoon and completely clears out the contents except for the old larval skin.

The predatory bug is sometimes present in considerable numbers on the leaves, but the adult was never observed. The nymphs are general predators and always seek their prey on leaves which are in the sun, and since all the food-plants of *A. trisignata* are nearly always in the shade, the bugs play little part in its control. Nevertheless on those few *Nicolaia* plants which do grow in the sun the bug kills very large numbers of larvae. It walks about the leaves with a larva stuck on the end of its rostrum. Larvae of all ages are attacked.

On one occasion the minute brown ant was seen in great numbers feeding on young larvae which emerged from eggs on the previous day. All the larvae on the leaf were destroyed. This happens very rarely, however.

The Clerid beetle was observed attacking the larvae on two occasions only and is of no importance. It is not the same species as the one that attacks *Artona catoxantha*.

The larvae of a Syrphid fly were found in large numbers attacking the young larvae at Tjibodas on Mt. Gede.

Ptychomyia remota rarely parasitises this host. It forms its puparium inside the cocoon.

Apanteles artonae, which is one of the most important parasites of *Artona catoxantha*, attacks *A. trisignata* very rarely. It has been reared on it in captivity, however.

Chalcid D is an external parasite of *A. trisignata* bred by Mr. S. Leefmans. It was never found by the writer.

The species of *Mesostenus*, which attacks *A. catoxantha*, was frequently bred from the cocoons, but was not considered of any economic importance. The same applies to Ichneumon A.

Chalcid B alone plays a much more important part in controlling this Zygaenid than all the other natural enemies together. All the others, with the possible exception of the egg parasite, are too spasmodic to be of any great value as controlling factors. Chalcid B is the only one that appears to confine itself entirely to the Zygaenid.

3. ARTONA (HOMOPHYLOTIS) ALBICILIA, Hamps. (Plate XXXI, Fig. 4)

Systematic

1. Hampson, *J. Asiat. Soc. Bombay*, 1900, p. 225.
2. Jordan, *Seitz. Macrolepidoptera of the World*, X, p. 46.

Range

* Island of Ron, Fergusson, Tenimber, Amboina, Pulo Laut, South-East Borneo, Java, North-East Assam.

In Java this Zygaenid was found only at Sindanglaja on the slopes of Mt. Gede at a height of 3,000 ft. We believe it to occur only in the mountains.

Food-plants

Hedychium and *Alpinia*. In the locality in which this insect was found in Java, many other genera of Zingiberaceae grew, in profusion, but it did not attack them.

Life-history

Egg.—The eggs are laid singly on the undersides of leaves of Zingiberaceous plants of the genera *Hedychium* and *Alpinia*. Several eggs may be laid on one leaf, but they are never grouped together. The egg is oval in shape when viewed from above, but it has a large depression on its upper surface which makes it somewhat crescentic when viewed laterally. The ends are rounded but are not hemispherical, and in a longitudinal section they are at right-angles to the plane of attachment to the leaf. The depression is a permanent feature of the egg and is not merely formed during the later stages of development of the contained larva. The colour is pale translucent green. The reticulations on the surface are extremely delicate and scarcely visible and are in the form of a regular network similar to that described for *A. trisignata*.

The incubation period is about seven days at an elevation of 3,000 ft.

Larva.—The young larva eats the lower epidermis of the leaf in straight lines between adjacent veins, but when it is half-grown, it strips the lower epidermis off in irregular wavy lines, and during the last two instars it usually eats right through the leaf at the edge. Its method of feeding is identical with that of *Artona catoxantha* and *Levuana*, the first thoracic segment forming a kind of sucker which is pressed against the leaf and completely covers the head. This structure is present throughout the larval life. The larva moults four times before it pupates. The duration of the first instar is three days, the second three days, the third three to four days (usually four), the fourth four days, and the fifth four days. The total duration of the larval stage is therefore eighteen days. These figures apply to larvae reared from eggs at Buitenzorg (*i.e.* at 600 ft. elevation), but the larval life is probably at least two days longer in the locality in which the eggs were found (*i.e.* 3,000 ft.).

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* [Dr. K. Jordan informs us that the moths under this name from these localities represent several distinct species—Ed.]

The older larvae always rest on the leaf in a very characteristic position and differ in this respect from the other species studied in connection with the *Levuana* work. The body is curved in a plane parallel to the leaf so as to take the form of a somewhat straightened letter S.

The colour of the young larvae is almost the same as that of the mature larva.

The full-grown larva is of a translucent green colour of the same tint as the underside of the leaf of *Alpinia* or *Hedychium.* The colour is usually uniform all over the body, but sometimes the thoracic segments are yellowish, and in the males the last four abdominal segments are whitish, while the first six abdominal segments may be blueish-green. The cuticle and body wall are semi-transparent and unpigmented, the colour of the larva being due entirely to the internal organs showing through the skin. There are no markings of any kind. There are four longitudinal rows of tubercles, each segment bearing one sub-dorsal and one lateral on each side. There are no tubercles on the first thoracic segment, and those on the last segment are fused together to form a large convex projection. The first thoracic segment forms a hood surrounding the head and is pressed against the leaf during feeding.

Cocoon.—The cocoon is placed on the underside of the leaf, usually against the midrib. It is identical in appearance with those of all the other Zygaenids studied in connection with *Levuana* and is formed in the same peculiar way. Like the others, it is covered with a fine white powder.

Pupation occurs two days after the cocoon is formed.

Pupa.—The pupa is of the typical Zygaenid form. It is very pale yellowish-green in colour until the day before the adult emerges, when it becomes very dark. The distribution of the spines on the dorsal plates of the abdomen is the same as in *A. trisignata* (*i.e.* on segments 3 to 7 in the female and 3 to 8 in the male), but the hooks which form the cremaster are different. Each hook is about half the size of that of *A. trisignata*, and there are about fifty altogether, *i.e.* more than twice as many as in *A. trisignata.*

The pupa pushes itself halfway out of its cocoon when emergence is about to take place, and the adult appears immediately. The time that elapses between the formation of the cocoon and emergence is nine or ten days.

Adult.—The adult is very similar to *Levuana* in general appearance and rests in the same characteristic attitude. Both sexes fly by day. Copulation was not observed, but evidently takes place on the same day as emergence, since oviposition begins early on the following day. The moths feed in captivity on honey and water. They will not oviposit in glass jars but will do so in large cages, provided that they contain a good supply of the food-plant and stand in a well-lit spot out of the direct sun.

The Life Cycle may be summarised as follows :—

Incubation of egg	7 days.
First instar	3 ,,
Second instar	3 ,,
Third instar	4 ,,
Fourth instar	4 ,,
Fifth instar	4 ,,
Pupal stage (formation of cocoon to emergence)	9 ,,
Emergence to oviposition	1 day
Average total	35 days
Range	33–37 days.

NATURAL ENEMIES

The only parasite which was found to attack this Zygaenid is *Apanteles taylori*, Wilk., which is almost identical with *Apanteles artonae* infesting *Artona catoxantha.* The comparative scarcity of the Zygaenid and the remoteness of the only locality known for it made a thorough investigation of the natural enemies impossible, but there is no doubt that the *Apanteles* is the only parasite that is of any economic importance. No predators were observed.

In July 1926, fifty-three larvae of the Zygaenid were collected and forty-four of these were parasitised by *Apanteles.* This proportion of parasitised larvae, which amounts to 83 per cent., was the highest observed.

Apanteles taylori, Wilk.,* has been reared only from *Artona albicilia.* It is almost certain that it is not present in Java below 2,000 ft. Its habits are identical with those of *Apanteles artonae*, but its life-cycle is about a week longer, as might be expected from the much lower temperature that prevails above 2,000 ft. The pupal stage is five and a half to six days, and the duration of the life-cycle from oviposition to emergence is approximately three weeks.

IMPORTANCE OF *ARTONA ALBICILIA* AS AN ALTERNATIVE SOURCE OF *APANTELES*

At the time when *A. albicilia* was first discovered in Java the *Apanteles* which attacks it was believed to be the same species as that which infests *Artona catoxantha.* The latter was then very scarce, and therefore *A. albicilia* was considered of importance as an alternative source of *Apanteles* for importation into Fiji. The fact that the *Apanteles* sp. from *A. albicilia* has since proved to be a new species is of little importance so far as *Levuana* is concerned because it is just as likely to attack *Levuana* as is *Apanteles artonae.*

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* Wilkinson, *Bull. Ent. Res.*, xix, 1928, p. 93.

4. ZYGAENID F. (*Artona* sp.) (Plate XXXI, Fig. 6)

SYSTEMATIC

This species, which is very similar in general appearance to *A. catoxantha*, is new and has not yet been described.

RANGE

Known only from Sindanglaja on Mt. Gede in Java, at a height of 3,000 ft. It probably only occurs at high elevations.

FOOD-PLANTS

This Zygaenid feeds on at least two different species of the genus *Costus*, and is probably confined entirely to plants of that genus. In the locality where it was found there was an abundance of other Zingiberaceous plants (*Alpinia*, *Nicolaia*, *Achasma*, and *Hedychium*), but they were never attacked by it. All of them are very different in appearance from *Costus*.

LIFE-HISTORY

Egg.—The eggs are laid singly on the undersides of the leaves of *Costus*. The largest number of eggs found on one leaf was three. The egg is pale green, dome-shaped, and perfectly circular in the plane parallel to the surface of attachment. The base is flat, and its diameter is considerably less than the greatest diameter of the egg. The plane of the greatest diameter is situated at about a quarter of the height of the egg from the base, and that part of the egg above this plane is practically hemispherical. The egg-shell is reticulated in the manner described for *A. trisignata*, but the network is more delicate than in the latter.

The incubation period is about six days.

Larva.—The young larva is pale green and is almost identical in appearance and structure with the young larvae of all the other Zygaenids studied in connection with *Levuana*. The hood-like first thoracic segment is well developed even in the newly hatched larva, and persists throughout the larval life. The larva strips off only the lower epidermis of the leaf until it reaches the fourth instar, when it begins eating right through the leaf. It does not feed in straight lines, however, probably because of the extreme fleshiness of the leaves of its food-plant which allows it to bite through the veins. The young larva remains a uniform pale green colour until the third moult, when the colouring of the full-grown larva begins to appear. There are four moults before pupation. The duration of the first instar is three days, of the second three days, the third three days, the fourth four days, and the fifth five days. The larval period, therefore, covers about eighteen days, as in *A. albicilia*, but the material available was insufficient to determine to what extent the rate of development varies. The larva rests in a straight position on the leaf and always remains on the underside.

The full-grown larva is strikingly marked with white and dark transverse rings. The thoracic segments and the last three abdominal segments are yellow or yellowish-green. The remainder of the body is dark brown and white in alternate transverse rings, each segment having a dark ring in the centre with a white ring in front and behind it. There is also a dark ring between the segments. All the rings are approximately equal in width. The tubercles are arranged in four longitudinal rows, there being four on each segment except the first thoracic which has none and is in the form of a hood covering the head. The tubercles on each segment consist of one sub-dorsal and one lateral pair and are situated on the middle ring. All the tubercles are black except on the yellow end-segments where they are yellow or brown, and each one bears a tuft of long hairs. The coloured markings do not extend down below the level of the spiracles. The ventral surface is of a uniform grey-brown colour.

Cocoon.—The cocoon was never observed in the field, but was formed on the underside of the leaf in captivity. It is very slightly larger and whiter than the cocoons of the other Zygaenids of the *Artona-Levuana* type, but otherwise it is identical with them, and it is formed in the same peculiar manner. Its extreme whiteness is due to the fact that the powdery deposit on its outer surface is unusually thick.

Pupa.—The pupa also is very similar to those of the other Zygaenids of this type, but the teeth on the abdominal segments and the cremastral spines serve to distinguish it. Only the female pupa was available for examination. The teeth are arranged in a single straight transverse row as in the case of the female *A. catoxantha.* The hooked spines which form the cremaster are arranged in three groups and are of a characteristic shape. The larger group, which is the most posterior, contains about ten spines, while the two smaller groups, which are slightly in front and to the side of the larger group, contain only two or three spines each. Each spine has a straight stem which is rather swollen in its distal half, and the tip is bent to form a minute hook.

The pupa turns almost black on the day prior to emergence of the adult, and pushes itself partly out of the cocoon when mature.

Emergence takes place eleven days after the formation of the cocoon.

Adult.—The adult emerges as soon as the pupa pushes itself out of the cocoon. In general appearance, as regards both colour and resting attitude, it is so similar to *Levuana* and *A. albicilia* that it would be scarcely possible to distinguish living individuals from one another at a short distance. The purple sheen, however, is much richer in *Levuana,* which also differs in the colour of the abdomen, but the latter is hidden when the moths are at rest. After death, these three species look much more different on account of the varying extents to which the colouring fades. In fact, the blue sheen of Zygaenid F disappears almost completely after death so that the insect comes to look much more like *A. catoxantha* than *Levuana.*

The adults fly by day.

No attempt was made to breed a second generation in captivity, and therefore nothing is known concerning the periods that elapse between copulation and oviposition in this species, nor were any natural enemies found.

The Life Cycle may be summarised as follows :—

Incubation of egg	6 days.
First instar	3 ,,
Second instar	3 ,,
Third instar	3 ,,
Fourth instar	4 ,,
Fifth instar	5 ,,
Pupal stage (from formation of cocoon to emergence)	11 ,,
Total	35 days.

(The total does not include the time from emergence to oviposition.)

5. ZYGAENIDS IN THE NEW GUINEA REGION

The larvae of five different Zygaenid species of the general *Artona-Levuana* type have been found in the New Guinea region, in which we include the Bismarck Archipelago and the Solomon Islands. These have been called Zygaenids B, C, D, X, and Y. Zygaenid X is the only one of which adults were reared, but it is not yet named. All of them feed on monocotyledons.

Zygaenid B was found near Rabaul in New Britain. It feeds on large species of Zingiberaceae of the *Nicolaia* type. The larvae are very similar to those of *A. albicilia.* They are attacked by a Chalcid ectoparasite which is very near to, if not identical with, Chalcid B of Java. The habits of this parasite are the same as those of Chalcid B in Java.

Zygaenids C and D were both found in the forest on the north coast of New Guinea, near the Dutch border. Zygaenid C feeds on a palm of the genus *Licuala*, and Zygaenid D on a palm similar to *Areca.* The investigations in New Guinea and the Bismarcks were made during the wet season, and the scarcity of all these Zygaenids at that time was very noticeable. In many localities their food-plants bore abundant feeding marks that were almost certainly made by them, or by closely allied species, a few months previously, but only in the localities mentioned were any larvae found, and even in those places they were extremely rare. There is no doubt that the wet season affects these insects adversely, and it affects *Artona catoxantha* in the same way in Java. Several larvae were found killed by fungus on leaves of *Licuala*, but we doubt if fungus is the chief cause of their rarity. Feeding marks were found on many palms besides those mentioned. They were particularly abundant on *Metroxylon* at Aitape, and the larvae that caused them had certainly been very numerous there during the dry season. Coconuts, however, were entirely devoid of Zygaenid feeding-marks both in New Guinea and the Bismarcks. Evidently species that feed on coconuts are very rare or absent in those islands.

Zygaenid X, of which adults were reared, feeds on Zingiberaceae in the Solomons. It is similar to *Levuana* in general appearance and habits, but its larval and adult structure show that it is actually a species of *Artona* (or *Homophylotis*). It is attacked by several parasites.

Zygaenid Y, which is much nearer to *Levuana* than to *Artona*, feeds on *Musa* in the Solomons.

The cocoons of all these Zygaenids in the New Guinea region are of the same peculiar form as those of *Levuana*.

The results of our search for Zygaenids of the general *Artona-Levuana* type in the New Guinea region were disappointing in many respects and were for the most part of a negative nature. The information obtained about the few species that were discovered was very scanty, and the pressure of other work elsewhere made a thorough investigation impossible. Nevertheless, the observations made were sufficient to enable us to draw some useful conclusions, some of which have already been discussed in the section dealing with the relationships of *Levuana*. The results of the work in the New Guinea region may be summarised as follows :—

1. Coconut-feeding Zygaenids are either absent or very rare in that region.
2. All Zygaenids of the *Artona-Levuana* type in New Guinea are very rare during the wet season.
3. *Artona*-like species extend right through New Guinea and the Bismarcks to the Solomons.
4. *Levuana*-like species are present in the Solomons.
5. The majority of, if not all, the Zygaenids of the general *Artona-Levuana* type feed either on palms, Zingiberaceae, or *Musa*, and in this respect they agree with those found in the Malayan region.
6. All these Zygaenids are very efficiently controlled by natural means, and several species of parasites are known.

6. CONCLUSION

Several Zygaenids allied to *Levuana* are now known to occur in Malaya, Java, and the New Guinea region. Their more important parasites are also known. Methods of breeding the parasites in captivity and of dealing with them during a long sea voyage have been devised and tested with satisfactory results.

The Tachinid parasite, *Ptychomyia remota*, which was imported into Fiji in 1925, has so far proved itself capable of controlling *Levuana* without the assistance of other parasites, and there is now every prospect of its continuing to do so ; but if, in the future, it should prove necessary to import more parasites, the knowledge gained in Malaya, Java, and the New Guinea region makes future importations a comparatively easy matter.

AN ACCOUNT OF THE ZYGAENID PARASITE CHALCID B

SYSTEMATIC

Order—Hymenoptera.
Superfamily—Chalcidoidea.
Family—
This insect has not yet been identified, and is therefore known as Chalcid B.

RANGE

Chalcid B occurs in suitable localities throughout Java. Its distribution in Java seems to depend solely on that of its host, *Artona trisignata*, to which it appears to be confined in that country. Its altitudinal distribution extends, like that of its host, from sea-level to 5,000 ft. (Mt. Gede).

This parasite is probably identical with one that was attacking a small *Artona*-like Zygaenid in New Guinea. Although it is not definitely recorded from any locality except Java, it very probably extends throughout the East Indies from Malaya to New Guinea.

HOSTS

In Java Chalcid B is a primary ectoparasite of *Artona trisignata* and is not known in nature from any other host, though it probably attacks other species of *Artona* occasionally. There is no doubt that it does not attack Lepidoptera generally, and it is almost certainly confined to Zygaenids of the *Artona* type.

A parasite that attacks a species of *Artona* in New Guinea is very probably this species. The species of *Artona* is very similar to *A. albicilia*, and is certainly not *A. trisignata*.

In captivity Chalcid B attacked *Levuana*.

LIFE-HISTORY

Egg.—The egg (Fig. 107) is almost invariably laid on second-instar larvae, but has occasionally been found on larvae that have just begun the third instar. It is nearly always laid mid-dorsally between the fourth and fifth segments of the larva, the long axis of the egg being at right angles to that of the host. Eggs have been observed between the second and third, third and fourth, and seventh and eighth segments, but only in cases of superparasitism. The habits of the larva explain why the egg is usually placed between the fourth and fifth segments.

In shape the egg is an elongate oval, but the longitudinal axis is curved so that the curvature of the lower surface of the egg corresponds to the transverse curvature of the host. One end is slightly broader than the other, and a transverse section is nearly circular. The egg is attached to the host very firmly by a short stalk, or sometimes merely a disc, which is continuous with the egg-shell. The egg-shell is perfectly transparent, so that the development of the contained larva can be seen clearly. When first laid, the whole egg is so transparent and colourless as to be almost invisible, but it becomes whitish and translucent as the larva develops.

Superparasitism is extremely rare in nature, but frequently occurs in captivity. In connection with it, an interesting phenomenon was observed. All the eggs on one host develop normally until one of them hatches, but as soon as this occurs, the development of the others always ceases, and they never hatch. The one that hatches is the one that was laid first. Apparently the young larva injects into the host some fluid which is toxic to the other eggs, and this fluid then reaches the latter by diffusion through the egg-stalks. This is the only possible explanation, for no outside influence is exerted on the other eggs. Observations on this point were repeated whenever suitable host larvae were available, and the results were the same in every case. In this way, any ill effects that might result from competition are prevented.

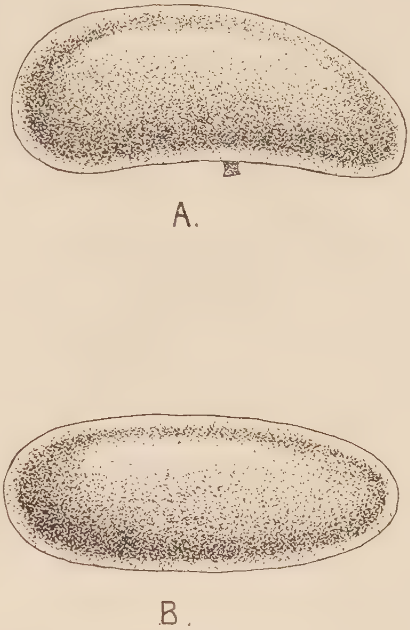

Fig. 107. — Chalcid B. — A. Lateral. B. Dorsal.

The host is paralysed by the female parasite at the time of oviposition, but it recovers a few minutes afterwards and usually continues all its normal activities until the egg of the parasite hatches. The duration of the egg stage in Java is about one and a half days—never as long as two days.

Larva.—As soon as the young parasite larva leaves the egg, it makes its way slowly down the side of the host between segments 4 and 5 and eventually takes up a position in the centre of the ventral surface, midway between the thoracic and abdominal feet. It was never observed to begin feeding until it reaches this position, but it must bite through the skin of the host as soon as it leaves the egg, because the activities of the host cease immediately the egg hatches, and it never moves again. The young larva begins feeding on the host as soon as it takes up its position between the latter and the leaf. Often the parasite appears to have inserted its anterior half into the body of the host, but this is not actually the case. This appearance is due to the invagination of the host skin by the parasite, but at no time is the body of the parasite actually inside the host. It presses its anterior end against the skin of the host and absorbs the contents of the body by suction, but no visible hole is ever made, the punctures being too minute for detection. If the parasite is removed, the skin of the host appears intact, and the contents cannot be squeezed out where the larva has been feeding. This process of absorption is made possible by the liquefaction of the organs of the host. The liquefaction begins as soon as the parasite leaves its eggs, and must be due to some substance injected into the body of the host by the parasite larva (not by the adult). The prolegs of the host remain attached to the leaf for some time after the parasite begins feeding, and there is not room for the latter to move along between the host and the leaf until it has absorbed a considerable amount of the body contents. This explains why the egg is nearly always laid between segments 4 and 5, for if it were laid anywhere else, the resulting larva could not take up its ventral position ; the only place where there is space enough for it to reach that position being beneath the first two abdominal segments, which are without legs.

The parasite grows very rapidly, and by the time it is half-grown, it can move freely beneath the host. It usually orientates itself so that its anal end is near the anus of the host, and the rest of the body extends forwards towards the head of the host. As it grows, the prolegs of its host become detached from the leaf, but the skin fits closely over it and is never perceptibly broken. The parasite is quite invisible from above, and its presence can only be detected by the appearance of its host, which becomes translucent and much darker than healthy larvae of the same age. This change in the appearance of the host is due to the liquefaction of the body contents and is of great importance when the parasites are being collected in the field, as parasitised larvae can be distinguished at once by means of it.

When the parasite is full-grown, it usually extends from the posterior extremity of the host to the second thoracic segment, whatever the size of the host may be. The whole of the contents of the body are removed, and the parasite larva lies in the space formerly occupied by the abdominal cavity, though it is actually outside the skin of the host. The abdomen is emptied completely so that the ventral skin is in contact with the dorsal and the parasite is below both. The head is never attacked. Even at this stage, the position of the host is perfectly normal, though its colour is abnormal. It is not attached directly to the leaf, and it is only the extreme stickiness of the skin of the Chalcid B larva which prevents both parasite and host from falling to the ground.

The full-grown larva (Figs. 108 and 109) is translucent and practically colourless. The cuticle and body-wall are perfectly transparent, so that those internal organs, including the cerebral and thoracic ganglia of the nervous system, which are not obscured by the very extensive and prominent fat-body, can be seen exceptionally clearly by transmitted light. The body is somewhat elongated, and the anterior end is rounded. The fifth segment is the widest, and behind it the body tapers regularly to a blunt point at the posterior end. The larva lies with its back in contact with the leaf, and the dorsal surface is consequently absolutely flat, while the ventral and lateral surfaces, which are covered by the skin of the host, are strongly convex. (The fact that it is the dorsal surface that is flattened is very deceptive at first glance, because the general appearance of the larva is such that the flat surface is interpreted as ventral until the relative positions of the internal organs are investigated.) There are fourteen well-marked segments, the first of which bears the mouth and a pair of papillae, and can be invaginated into the second, while the anal (fourteenth) segment is tubular and very small. Each of the segments from the fourth to the eleventh bulges out on either side at the point where the lateral surface joins the flat dorsal surface. The prominences so formed are very characteristic and make the segmentation very obvious. They appear to function as prolegs, since it is by means of them that the larva grips the leaf when moving up and down, or turning round beneath the host. They bear no chitinous hooks, or other special structures

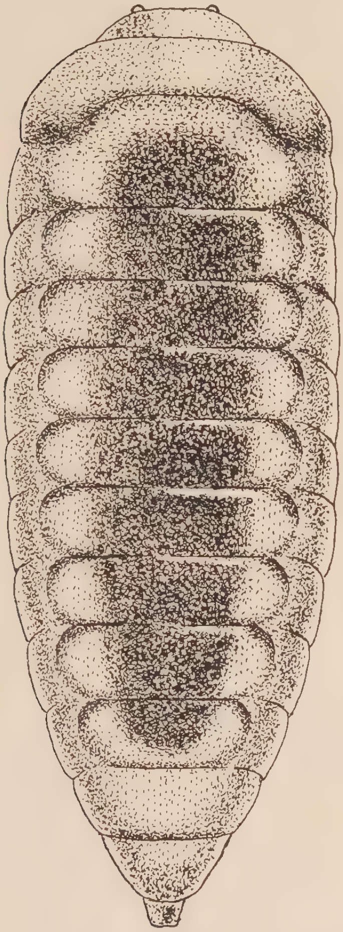

FIG. 108.—Chalcid B.—Full-grown larva (dorsal view). × 60.

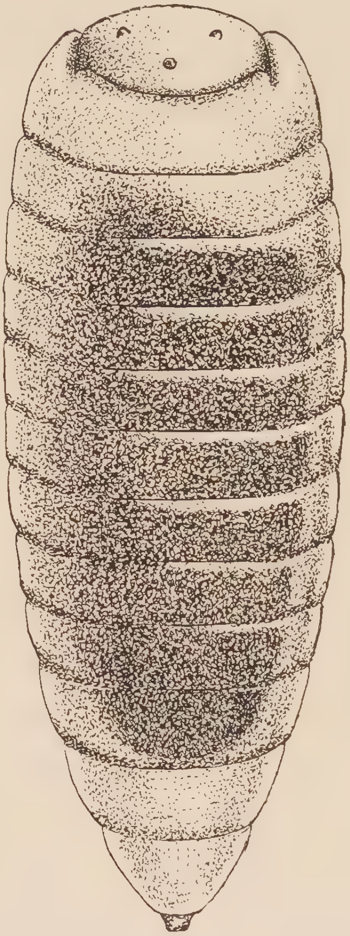

FIG. 109.—Chalcid B.—Full-grown larva (ventral view). × 60.

for gripping the leaf, but they are glandular and produce a sticky secretion that serves the same purpose. This, therefore, is an instance of a larva whose organs of locomotion are dorsal to the spiracular line.

The stomach is very obvious as a dark brown ovoid mass extending from segments 3 to 11, but it is not clearly outlined on account of the density of the surrounding fat-body. Its colour is due entirely to its food contents. The oesophagus does not retain any of the food that is passed down it into the stomach, and therefore it is very transparent, and only faintly visible. The anus is not perforated until the larva is full-grown. The tracheal system is well developed on account of the external habit of the larva. There are always nine pairs of spiracles, one pair on each segment from 3 to 11. The spiracles are situated mid-laterally, near the anterior edges of their respective segments. There is one main tracheal trunk, with which the spiracles are directly connected, on either side. The two main trunks are connected by a transverse trachea, dorsal to the oesophagus, in the second segment, and by

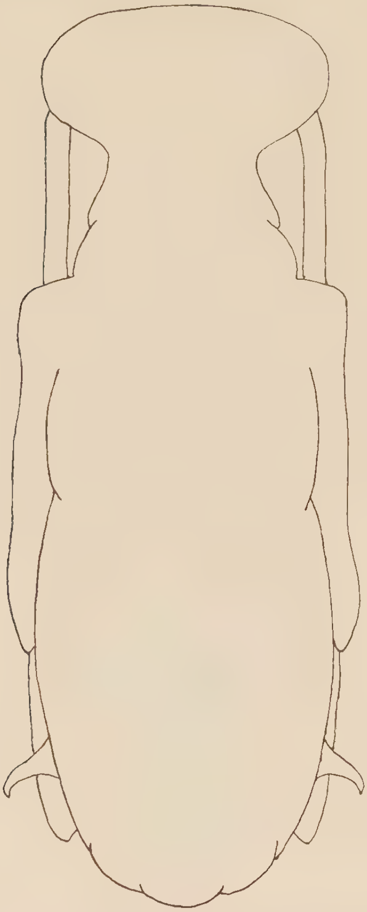

Fig. 110.—Chalcid B.—Outline of pupa (dorsal). × 75.

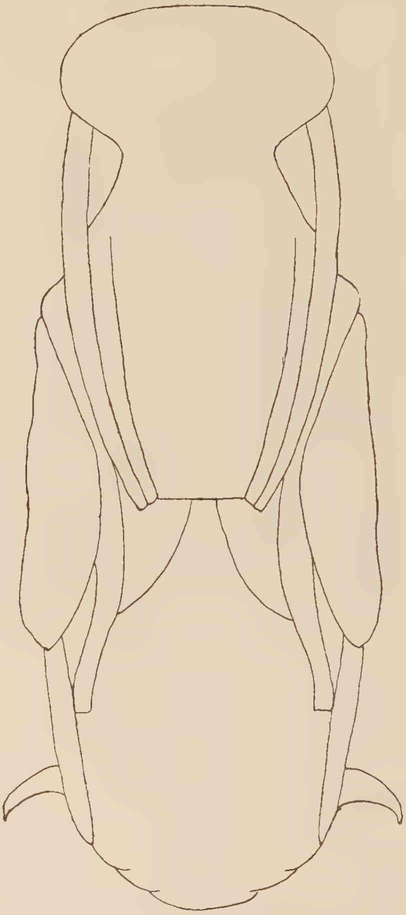

Fig. 111.—Chalcid B.—Outline of pupa (ventral). × 75.

another dorsal to the rectum, in the twelfth. The fat-body is very dense, and extends without interruption from the third segment to the thirteenth, and often extends forwards into the second. The mouth, on the first segment, is nearer the ventral than the dorsal edge of that segment, while the two papillae, which are on the same segment, are nearer the dorsal edge. Each papilla consists of an almost flat, slightly convex, disc with a very obtuse point in the centre, and is merely a chitinous thickening of the cuticle. The papillae do not appear to have any sensory function, but serve rather to hold the head in place when it is pressed against the surface of the host for feeding purposes. The mouth-parts are prominent, though very small. They consist of a pair of brown, strongly chitinised mandibles and a curved bar which borders and supports the mouth opening on its dorsal side. The curved bar is merely a thickening of the cuticle. Each mandible consists of a sharp point projecting from one corner of a triangular base, which is nearly equilateral. The smooth curved bar and that part of the ventral surface that borders the mouth posteriorly form a sucker which closely adheres to the host skin and enables the larva to absorb the liquid contents of the body of the host through minute punctures made by the mandibles.

The average length of the full-grown larva is 2·04 mm.

No defaecation occurs until the larva is mature, but just before it pupates it thrusts its terminal segments out from beneath the skin of the hind end of the host and emits a series of round faecal pellets which are sticky and so remain attached in turn to the anus. Each one pushes its predecessor in front of it, but remains attached to it, and in this way a spirally-coiled chain of faeces is formed outside the skin of the host and serves as a check on the rate of development of the parasite. The chain usually consists of sixteen pellets which are produced at a uniform rate of one every three minutes approximately, the whole process occupying nearly an hour. This is the only occasion on which the parasite is visible from the outside.

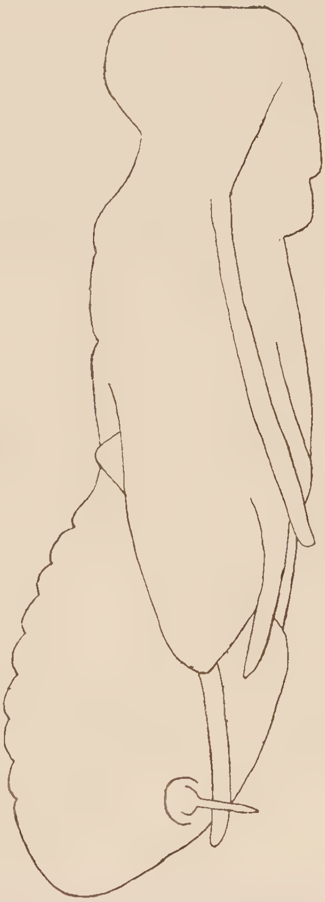

Fig. 112.—Chalcid B.—Outline of pupa (right lateral). × 75.

The duration of the larval stage varies from three to five days at Buitenzorg, four and a half days being the most common period.

Pupa (Figs. 110, 111 and 112).—Pupation occurs on the day following excretion. The pupa is of a light rich brown colour and is semi-transparent. It is somewhat flattened and is almost rectangular in outline when viewed dorsally or ventrally. Its average length is 1·56 mm. The sheaths of the adult appendages are closely apposed to the ventral surface, but are not attached to it, except at their bases. The only unusual feature of the pupa is a very prominent, sharp pair of strongly chitinised hooks near the posterior extremity. Each hook arises laterally from the seventh and eighth abdominal segments ; its base is broad, and it curves towards the ventral surface of the pupa.

The pupa is completely covered by the skin of the host, which extends down the sides of it almost to the leaf. The skin of the host remains soft until the parasite pupates, but it dries soon afterwards and contracts at the same time, so that it fits the pupa very closely. The pupa is in such a position that its dorsal surface is in contact with the leaf, and it extends from the thoracic segments of the host to the anal extremity, but it is attached to the leaf posteriorly only by the sticky cast skin of the larva, and there is no other means of attachment. The head of the pupa invaginates the anterior thoracic segments of the host from behind and below, and is therefore held in place.

When the pupa, and the host skin which covers it, are viewed from above, the two hooks appear to penetrate the host skin laterally, and to attach it to the pupa, but a closer examination shows that the skin of the host extends down on each side as far as the base of the hook and no further, so that it is not actually pierced at all. The hooks, therefore, do not serve for attachment to the host skin. Their true function appears to be respiration, for when the pupa is suitably stained, a tracheal trunk can be seen extending along the axis of each hook and terminating in a spiracle at its tip. This apparatus is apparently necessary on account of the presence of the closely fitting host skin which would make any other spiracles useless. No modification is present in the larva because the spiracles are not blocked until the host skin dries and shrinks.

The pupa turns black one day before the emergence of the adult. The duration of the pupal stage is five and a half days.

Adult.—The adult emerges by bursting the pupal skin on the dorsal side of the head and thorax, and then crawling out between the host skin and the leaf. The position of the pupa suggests that the adults must emerge by biting a hole through the host skin, but this never occurs.

Copulation occurs on the day of emergence or on the following day, but oviposition does not begin until at least five days after emergence. Parthenogenesis occurred in captivity and is arrhenotokous.

When about to oviposit on a larva, the adult parasite approaches it slowly and hesitatingly. The antennae vibrate very rapidly, and as soon as they come in contact with the hairs of the larva, the latter turns away sharply and the parasite withdraws. Several more attempts are usually made before the parasite accomplishes its object. Eventually it darts very suddenly on to the back of the larva and stings it, and lays a single egg with extraordinary rapidity, the whole process apparently being completed in one movement and occupying about one second. The parasite then walks off and the larva remains paralysed for about three minutes, after which time it recovers and pursues its normal activities. The stinging has no permanent effect on the larva, for if the egg of the parasite is removed with a needle before it hatches, the larva develops normally and eventually produces an adult. The death of the host larva is therefore entirely due to the newly-hatched parasite.

Very frequently, the adult Chalcid B feeds on a larva of *Artona trisignata* after stinging it and ovipositing on it, but in such cases it stings the larva again after egg-laying and the ovipositor usually remains inserted into the larva for at least ten minutes. The parasite then walks on to the leaf, strolls round the larva, and then approaches it again. Finally it bites the larva on the side of one of the thoracic segments, and sucks out the body fluid. The larva never recovers, and though the egg on its back hatches, the resulting parasite larva never matures, because its host shrivels and dries up.

This feeding habit of the adult parasite is important from the point of view of the control of the Zygaenid, because larvae which have not had eggs laid on them are very frequently bitten by the fly and are consequently killed. Large numbers of larvae are killed in this way, both in the field and in the laboratory, and in some broods the number of larvae killed through being bitten and sucked by the flies is as great as the number killed by the parasite larvae.

Female flies that have laid all their eggs frequently continue to sting larvae for a long time after they have ceased ovipositing. In one such case, a fly stung a larva four times in succession, the ovipositor remaining inserted in the larva for twenty minutes the first time, and for five minutes each following time. So much fluid was pumped into the larva that its body swelled up enormously, and when the ovipositor was withdrawn, the fluid gushed out through the perforation in the skin. No eggs were laid, and the fly did not feed on the larva. The larva did not recover until half an hour later.

The male Chalcid B dies from three to five days after emergence, but the female seems capable of an almost indefinite existence, provided it has not laid many eggs. In captivity, many females were kept alive for six weeks, and in nature they probably live three months at least. If they are entirely restricted to Zygaenids of the *Artona* type, as they appear to be, it is very necessary for them to live a long time, as their hosts are often absent for many weeks in localities where they were formerly common. One female which had been kept apart from the larvae of its host for a month, oviposited readily as soon as it was provided with larvae.

There is no doubt that in nature the Chalcids feed to a considerable extent on the larvae of their host, but in captivity they thrive on honey and water, or sugar and water only.

The Life Cycle at Buitenzorg may be summarised as follows :—

Incubation of egg	1½ days.
Duration of larval stage	3–5 days.
Duration of pupal stage	5–6 days.
Emergence to oviposition	Not less than 4 days.
Total (oviposition to emergence)	(Average) 12 days.

No doubt development is much slower at higher altitudes.

NATURAL ENEMIES

Chalcid B has only one parasite in Java, and nothing is known about its natural enemies elsewhere. This one parasite is Chalcid A, a hyperparasite of *Artona trisignata* through Chalcid B. It appears to be confined entirely to Chalcid B. It kills large numbers of Chalcid B, and greatly diminishes the efficiency of the latter in controlling the Zygaenid. Its life-history was therefore studied sufficiently to ensure its elimination when Chalcid B was imported into Fiji. The reduction in efficiency of Chalcid B by Chalcid A is discussed on p. 241. A brief account of the habits of Chalcid A, which has not yet been named, follows. (See Figs. 113, 114 and 115.)

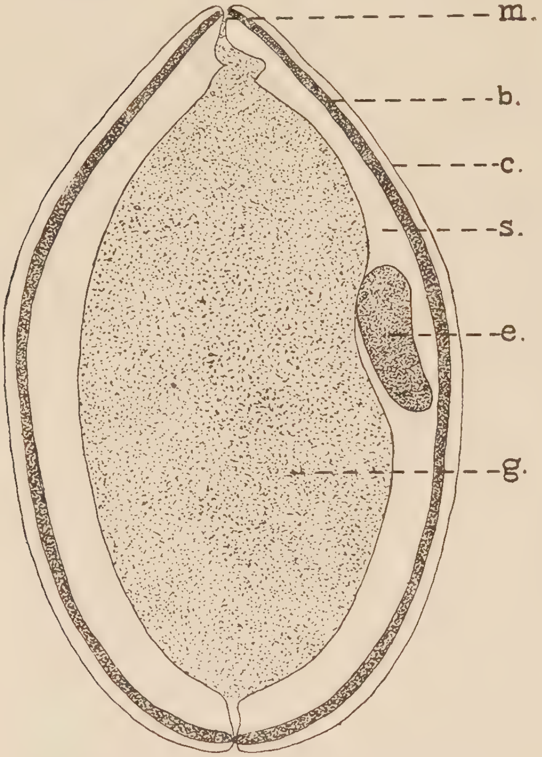

FIG. 113.—Egg of Chalcid A in young larva of Chalcid B (diagrammatic). *b.*, body-wall of Chalcid B larva; *c.*, cuticle of Chalcid B larva; *e.*, egg of Chalcid A; *g.*, gut of Chalcid B larva; *m.*, mouth of Chalcid B larva; *s.*, space occupied by fat-body.

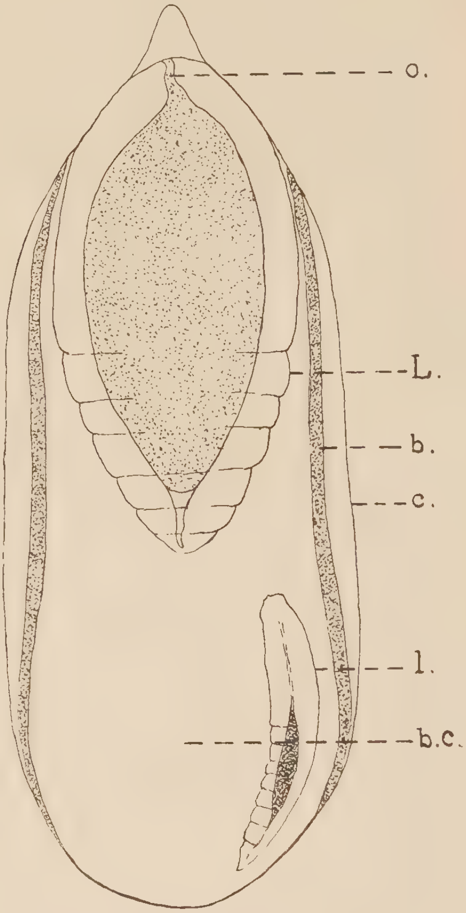

FIG. 114.—One full-grown and one young larva of Chalcid A in half-grown larva of Chalcid B (diagrammatic). L. full-grown larva of Chalcid A; *l.*, young larva of Chalcid A; *o.*, oesophagus of Chalcid A larva; *b.c.*, body-cavity of Chalcid B larva emptied by Chalcid A. (Other lettering as in Fig. 41.)

The egg of Chalcid A is very minute. It is shaped exactly like the egg of Chalcid B and is very transparent. It is laid inside the body of the larva of

Chalcid B between the gut and the body-wall, never between the body-wall and the cuticle. It is quite free within its host and its position is constantly changed by the movements of the gut of the host. Any region of the body of the host may be selected by the parasite for oviposition, but the posterior end is preferred. The larva of Chalcid B is liable to be attacked as soon as it is one and a half days old, but not before. The duration of the egg stage is about two days.

The young larva begins feeding on the fat-body of the host as soon as it leaves the egg. It is extremely active and moves from end of the host very rapidly by constantly bending and straightening itself. It grows quickly, but its presence does not hinder the growth of the host. It devours the fat-body and the rudimentary gonads, but never attacks the alimentary canal or the nervous system until it is full-grown. Its activities can be watched very easily on account of the great transparency of the Chalcid B larva.

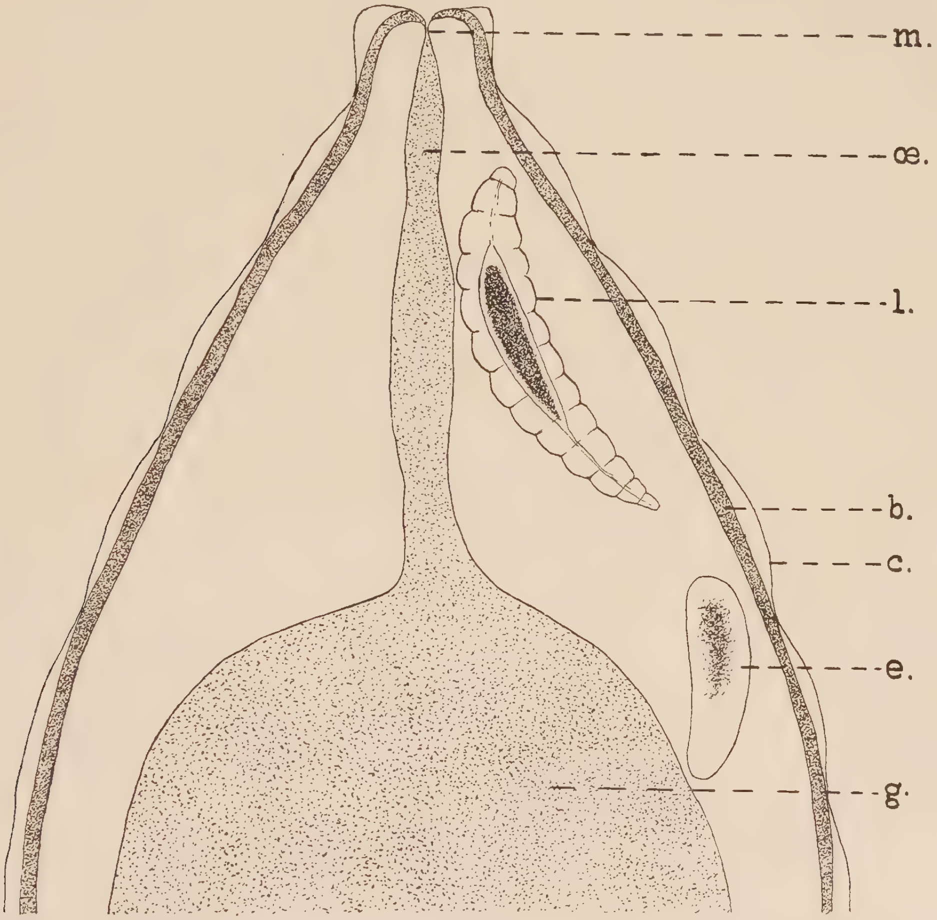

Fig. 115.—Egg and young larva of Chalcid A in full-grown larva of Chalcid B (diagrammatic). *œ.*, oesophagus of Chalcid B larva. (Other lettering as in Fig. 41.)

The full-grown larva of Chalcid A is rather more slender than that of Chalcid B. It consists of thirteen well-marked segments. The gut is very clearly seen, but the other organs are so transparent as to be almost invisible.

The duration of the larval stage is five days.

When the larva is mature, it kills its host, devouring all the internal organs and leaving only the cuticle. The stage of development reached by the host varies according to its age when the egg of Chalcid A was laid in it. If a Chalcid B larva is attacked when it is about a third grown, it completes its growth but is killed before it can pupate ; if it is attacked when it is half-grown or more, it invariably pupates, but no further development occurs. In nature the great majority of Chalcid B larvae which are parasitised by Chalcid A pupate before they are killed.

As soon as the Chalcid A larva has devoured the whole of the body contents of the host it excretes. No excretion occurs until this stage is reached. The complete absorption of the body contents causes the skin to dry up and become very brittle, but it retains its original shape, no matter whether it was a larva or a pupa before it was killed. The pupa of Chalcid A therefore lies in the space enclosed by the dried, brown, transparent skin of the host, and since it only occupies about half that space, it rattles freely within it.

Superparasitism of Chalcid B by Chalcid A occurs very frequently, and in such cases all the eggs of Chalcid A laid in one host hatch, unlike those of Chalcid B in similar circumstances. As many as seven eggs of Chalcid A may be laid in one larva of Chalcid B, but they are in different stages of development and are probably laid separately by different parents. In other cases eggs of Chalcid A are laid in Chalcid B larvae which already contain larvae of Chalcid A. In all cases of superparasitism, however, only one parasite matures in each host, all the others dying when they are very small larvae.

The pupa of Chalcid A is entirely different in appearance from that of Chalcid B. It is black, strongly chitinised, opaque, and very obtected. Its position is such that its anal extremity is in contact with the same extremity of the host skin, and its length is about two-thirds of that of its host. The skin of the Zygaenid larva covers both.

The duration of the pupal stage is six days.

The adult Chalcid A emerges by splitting the skin of the head of its host and then crawling out beneath the skin of the Zygaenid larva. Copulation was not observed. The females live a long time—three weeks at least—and feed readily on honey or sugar in water.

Inter-relations of Chalcid B and Chalcid A

Chalcid B controls an outbreak of *Artona trisignata* before the supply of the food-plant is exhausted, but it takes a long time to do it, and the delay is due to the presence of Chalcid A.

In an outbreak of *A. trisignata* under special observation, Chalcid B reached its maximum abundance after six broods of the Zygaenid and with the assistance of predators the outbreak was completely stopped. But during the last brood of the Zygaenid, Chalcid A reached its maximum also and Chalcid B was completely wiped out; that is to say, Chalcid B only just managed to suppress the Zygaenid before it (Chalcid B) was itself wiped out by Chalcid A, and if Chalcid B had been suppressed one generation sooner, the Zygaenid would then have been able to multiply to an almost indefinite extent until it was discovered by more Chalcid B from another locality. The fact that the suppression of the Zygaenid synchronised with that of its suppressor in the particular outbreak observed implies that Chalcid B multiplies more rapidly than the Zygaenid, while Chalcid A multiplies more rapidly than either, and it is also clear that if the activity of Chalcid B had not been hindered by Chalcid A the outbreak would have been stopped much sooner than was actually the case. As a result of the simultaneous disappearance of the Zygaenid and its primary parasite, the secondary parasite, Chalcid A, must itself be destroyed, since it has no host individuals on which to rear another generation. It is very doubtful whether either Chalcid A or Chalcid B had any alternative hosts in the locality where the outbreak occurred.

The complete and simultaneous suppression of both Chalcid B and its host is probably very unusual. It much more frequently happens that Chalcid B wipes out the Zygaenid before it (Chalcid B) is itself exterminated. In this case a number of individuals of both Chalcids B and A survive, and these presumably migrate to other outbreaks of the Zygaenid elsewhere. The long adult life of these two parasites makes extensive migrations possible, and there is no doubt that they occur. Chalcid B is invariably absent in the first generation of the Zygaenid in a new locality, and often in the second generation also, yet it always appears before the outbreak is very far advanced.

It occasionally happens that when an outbreak of the Zygaenid is almost completely suppressed no further suppression takes place. The Zygaenid maintains itself in small and more or less constant numbers for several more generations and then begins to multiply rapidly again. Such an instance was observed in an isolated locality in the Botanical Gardens, Buitenzorg. This appears to be a case in which Chalcid A exterminated Chalcid B before the latter exterminated the Zygaenid, so that the Zygaenid, although suppressed, was not wiped out entirely and was subsequently able to recover itself.

This Zygaenid complex is particularly interesting in that it shows to some extent how important a part a secondary parasite may play in regulating the occurrence and periodicity of outbreaks of a pest. The fact that the Zygaenid is not attacked to any great extent by any other parasites besides Chalcid B makes it much easier to study the relative effects of its primary and secondary parasites than is usually the case, and it would be profitable to make a more extended investigation of the matter if opportunity offers.

The feeding habits of the adult Chalcid B greatly increase its efficiency as a control for *A. trisignata* and must not be overlooked in this connection. The adults feed on the Zygaenid larvae, killing all they attack, and the number of larvae killed in this way appears to be nearly as great as the number killed by parasitism. This unusual habit increases the efficiency of the parasite sufficiently to neutralise the adverse effect of Chalcid A to some extent.

Breeding and Liberation of Colonies

Chalcid B is very easy to breed in captivity. The adults lay readily in tubes when provided with host larvae of a suitable age, and the parasitised larvae can be left in the tubes without attention until the parasites are mature, about twelve days later.

The method employed for the shipment from Java to Fiji was equally simple. A number of plants of *Nicolaia* were planted in tins and placed in a large wooden cage (6 ft. high ×4 ft. ×3 ft.) with glass windows. The plants were stocked with larvae of *Artona trisignata.* The parasites were shipped in the pupal stage, and the resulting adults were fed on sugar and water in glass tubes. Their host, *A. trisignata*, bred satisfactorily in the cage on board ship, and whenever larvae of a suitable age were available they were transferred to the tubes, and the parasites oviposited on them. The secondary parasite, Chalcid A, was therefore completely eliminated.

The scarcity of *A. trisignata* in Java at the time of sailing was the only difficulty. As a result of it, the supply of parasites was greatly reduced, and only fifty-eight pupae were shipped. Of these, fifty-six produced adults *en route* to Fiji; forty-two parasitised larvae were obtained from these on board, and every one of them produced an adult parasite in Fiji.

A smallpox outbreak on board the ship during the voyage necessitated a very strict quarantine in Fiji for five weeks after the ship arrived there. Many difficulties arose as a result of this, the greatest being that there was little or no *Levuana* on Nukulau, the quarantine island, at the time, and that no one who understood the work could visit the neighbouring quarantine island of Makuluva where *Levuana* was available.

A small supply of *Levuana* eggs was received from Suva and the resulting larvae were parasitised by Chalcid B on Nukulau. Twenty-three parasitised larvae of *Levuana* were thus obtained, and they all pupated in due course. Twenty of these parasites were sent over to Makuluva as pupae, and the remaining three were kept on Nukulau to make sure that Chalcid B could breed through satisfactorily on *Levuana.* All three produced healthy males, and there is very little doubt that the twenty pupae produced adults at Makuluva.

In the meantime six females of the original batch of parasites shipped in Java were liberated on Nukulau; and twenty-five of their progeny, which reached maturity on Nukulau, were sent to Makuluva, the remaining seventeen being retained for breeding on *Levuana.*

The total liberations (all in January and February 1926) were therefore as follows :—

Nukulau	6
Makuluva	20 pupae. 25 adults.

Recovery in the Field

Chalcid B has not yet been recovered in Fiji. Although the numbers liberated were small they should have been ample, provided that *Levuana* is attacked in the field as readily as *Artona trisignata*. It is possible, however, that the adults were carried away by the strong winds prevalent at the time.

TRICHOGRAMMATOIDEA NANA, THE EGG PARASITE OF JAVAN ZYGAENIDAE

Systematic

Order—Hymenoptera.
Superfamily—Chalcidoidea.
Family—Trichogrammidae.

Trichogrammatoidea (*Chaetosticha*) *nana*, Zehntner

Range

T. nana is recorded only from Java, and probably does not occur elsewhere. In Java, however, it is common and widely distributed, and it extends up the mountains to a height of 4,000 ft. (Tjibodas, Mt. Gede) and possibly higher.

Hosts

In Java *T. nana* is best known as a parasite of the eggs of various species of rice-borers (*Chilo*, *Schoenobius*, *Scirpophaga*). It undoubtedly has a great variety of hosts, and, judging from experiments made at Buitenzorg, it is capable of parasitising almost any kind of Lepidopterous egg provided that the egg-shell permits of the insertion of the ovipositor. The relative thickness and hardness of the egg-shell seems to be the only limiting factor. In Java, *T. nana* was reared in captivity in the eggs of two Pyralids, one Noctuid, one Lachneid, one Lycaenid, and two Zygaenids. The Zygaenids were *Artona trisignata* and *A. catoxantha*, the latter in the laboratory only, and the former in the field as well as in the laboratory.

T. nana is recorded from eggs of the following moths :—

1. *Diatraea striatalis*, Sn.
2. *Chilo infuscatellus*, Sn.
3. *Scirpophaga intacta*, Sn.
4. *Olethreutes schistaceana*, Sn.
5. *Schoenobius bipunctifer*, Wlk.

Life-history

In studying the life-history of this parasite, special attention had to be given to those points that were necessary for the discovery of suitable methods of breeding it in the laboratory and of shipping it to Fiji. The account of it given here is therefore incomplete. Further, the host eggs employed for breeding the parasite were nearly always those of species of *Artona*, so that the observations recorded below are directly applicable to those insects only, though most of them no doubt apply to the other hosts also. The most important point was the determination of the total duration of the life-cycle, and this was worked out carefully on Zygaenid eggs and checked on the eggs of a variety of Lepidopterous insects.

Egg.—The egg of *Trichogrammatoidea nana* is so extremely small that it is comparable in size to the yolk globules of the host egg which surround it. It is therefore very difficult to detect, especially as it is very transparent. Methylene blue was found very useful for staining it in order to make it more clearly visible. It is nearly spherical in shape, but is bluntly pointed at the two poles, in the vicinity of which the shell is greatly thickened. Its longest axis passes through the poles.

The puncture made in the host egg-shell during oviposition cannot be detected, but two or three days after the egg of the parasite has been laid the locality of the puncture is indicated by the formation of a minute black spot round the point at which the ovipositor was inserted. This black spot, which is always in the vicinity of the micropyle, is the first indication of parasitism, and as such is very useful during breeding experiments. Sometimes two spots appear at the same time, suggesting superparasitism, but their presence does not necessarily prove that the egg is parasitised, because the pigment spots on the head of a larva of *Artona* in a healthy egg have exactly the same appearance.

The incubation period of the parasite egg is about twenty-four hours only.

A few days after the egg of the parasite has been laid, the host egg appears to the naked eye to turn dark grey. This is due to the sudden formation of black streaks and patches which first appear in the neighbourhood of the black spot already mentioned and soon extend down the sides of the egg towards the other pole, while the general contents of the egg become greyish. This is the first sure sign of parasitism. The time that elapses between the laying of the parasite egg and the first appearance of these patches in the host egg was found to depend entirely on the degree of development of the host egg at the time when the egg of the parasite was laid in it. If the parasite attacks the host egg on the day it is laid, the latter turns grey four days later; that is to say, one day before the healthy Zygaenid eggs of the same batch hatch. It is only under these circumstances that it is possible to detect parasitism before the healthy eggs hatch. If the parasite attacks the Zygaenid eggs three or four days after they are laid, which is usually the case, they do not change their appearance until after the healthy eggs of the same batch have hatched, although the darkening begins much sooner, relatively, in an egg which was attacked only a short time before it was due to hatch than in one which was attacked soon after it was laid. Therefore the change cannot be regarded as an indication of the age of the parasite within and is due merely to a physiological condition of the normal contents of the host egg, a condition that is dependent on the age of the host egg and not on the age of the parasite. The fact that the darkening does not usually appear until after the healthy eggs have hatched is of importance when the parasites are being collected in the field.

Within one or two days after the dark patches first appear the whole egg turns quite black all over, and if it is dissected at this stage, the blackness is found to be due to a deposit of minute dark granules that form a continuous opaque layer all over the inside of the shell. This layer can be separated from the shell, leaving the latter quite clear and transparent, and it is apparently precipitated only from the outside layer of the fluid contents of the host egg.

So far as the development of the parasite is concerned, it is immaterial whether the host egg is attacked on the day it is laid or on any succeeding day up to twenty-four hours before it is due to hatch. When eggs are parasitised only a few hours before the young larvae are ready to emerge, most of the larvae do emerge but die the same day ; the remaining larvae do not emerge from the eggs and the parasites usually develop normally within them.

Occasionally two parasite larvae develop up to a certain stage within one host egg, but in such cases only one of them reaches maturity.

Larva.—The larva of the parasite is full-grown five days after the egg is laid. It is oval, sack-like, and nearly as broad as it is long. The cuticle is extremely thin and transparent, but the only organs that are clearly defined are the well-chitinised mandibles. Each mandible is in the form of a thin curved spine which tapers regularly to a sharp point at its extremity. The larva almost completely fills the Zygaenid egg, but until it is ready to pupate, the very small space between it and the egg-shell is occupied by a fluid in which are suspended innumerable, minute, fatty, non-cellular globules. These globules exhibit very marked Brownian movements if the fluid is squeezed out into a drop of water, but in addition to them the fluid contains minute protozoa of various forms, which are presumably of a phagocytic nature.

The larvae does not defaecate until it is full-grown.

Pupa.—The pupa, like the larva, is plump, thin-skinned, and transparent. Its head is usually at the micropylar end of the host egg, but it is sometimes the other way round.

The duration of the pupal stage is five days.

Adult.—The adult parasite appears six, seven, or eight days after the host egg turns grey. It makes an irregular hole in the egg-shell for its exit, and the position of the hole depends on the orientation of the pupa in the host egg. The female is probably capable of living for at least three weeks in nature, except when it lays all its eggs soon after emergence. Males live for as long as eleven days in captivity when not allowed to copulate, but die after four or five days if copulation has occurred. Oviposition begins on the day following emergence if suitable host eggs are available. Both sexes thrive on honey and water in captivity. Parthenogenesis frequently occurs and is arrhenotokous. The female sometimes inserts its ovipositor into eggs of the host without ovipositing, and in such cases the host eggs are killed. Each female keeps to one batch of eggs for some time, working over it systematically and continuously. In captivity parasitism is often very nearly total, and in one case it was absolutely total. In nature, parasitism occasionally reaches 60 per cent., but 30 per cent. is more usual.

The necessary conditions for oviposition by the parasite are either that the shell of the host egg be very thin or that the perforations at the micropylar end allow the ovipositor to pass through them. The adult is much smaller and more delicate than the other common egg-parasites in Java (*Trichogramma* spp., *Telenomus* spp., etc.), and it cannot oviposit in the eggs of some of the species that are regularly attacked by others. In order to obtain some idea of its range of hosts, a large number of moths of different species were collected at light at night and were then enclosed in match-boxes, in which many of them oviposited. Their eggs were then placed in glass tubes (one species per tube) with the female parasites. In every case, without a single exception, an attempt was made by the parasites to oviposit within a quarter of an hour after the eggs were put in the tubes, and was continued for two days, after which the eggs were removed. The eggs employed in the experiment included those of many different Noctuids, three Pyralids, a Lachneid, a Lasiocampid, and a Lycaenid butterfly. Most of these, however, proved to be too hard for the ovipositor to penetrate, and the only ones that were successfully parasitised were two of the Pyralids, one Noctuid, the Lachneid, and the Lycaenid. The case of the Noctuid was particularly interesting; there were about 200 eggs in the batch, and the parasites worked over the whole of it during the two days, apparently ovipositing in all the eggs, yet all except one of them hatched in due course and produced healthy Noctuid larvae. The one exception produced a male of *T. nana*. This indicated that the original parasites only succeeded in penetrating one egg out of 200, but it also shows that the parasite is capable of breeding in these eggs if it can manage to penetrate the egg-shell with its ovipositor.

The total duration of the life-cycle of the parasite for all these different hosts was found to be the same as for *Artona trisignata* and *A. catoxantha*, namely, ten days from oviposition to emergence.

T. nana has never been found to attack the eggs of *Artona catoxantha* in nature, but the great readiness with which it does so in the laboratory indicates that it must occasionally attack them under natural conditions.

On account of the great variety of hosts that this parasite possesses and its apparently general distribution throughout Java, it is probably always present in every locality where an outbreak of *A. trisignata* occurs. Nevertheless, it very rarely attacks the eggs of the Zygaenid during the first brood or two of a new outbreak, but as soon as it starts to attack them, it continues to do so until the outbreak is over.

Summary of Life-cycle.—The total duration of the life-cycle from oviposition to emergence is very constant at ten days as a rule, but in one batch the adults appeared nine days after oviposition.

The life-cycle may be summarised as follows:—

Incubation of egg	1 day.
Larval stage	4 days.
Pupal stage	5 ,,
Emergence to oviposition	1 day (minimum).

Breeding and Liberation of Colonies

The breeding of this parasite on a small scale in the laboratory is comparatively easy. On board ship, however, during the voyage from Java to Fiji, it was found much more difficult to breed, chiefly on account of its minute size and the necessity for providing the adults with Lepidopterous eggs immediately they emerged.

In Java, the most useful host eggs for obtaining *T. nana* are those of the rice-borers, of *Lampides boetica* on *Crotalaria* or of *Artona trisignata* on Zingiberaceous plants. (Except in the latter case, other egg parasites are likely to appear as well.) When the parasites emerge, they are enclosed in small glass tubes with a supply of healthy eggs of a suitable host. They must be fed twice a day on honey in water, and the supply of host eggs should be renewed every day if possible. The next generation of parasites will emerge from the host eggs ten days later.

During the voyage from Java to Fiji, the host employed for this parasite and for Chalcid B was *Artona trisignata*, which was bred in a large cage containing *Nicolaia* plants. This was the easiest host to deal with on a long sea voyage, but unfortunately at the time of sailing it was very scarce in Java, although it had been abundant a few months previously. Consequently, the number shipped was not sufficient to ensure an almost constant supply of eggs throughout the voyage. The majority of parasites bred *en route* died before eggs were available, though whenever eggs were supplied the parasites bred very well. At the latter end of the voyage one batch of twenty-five parasitised eggs, in which the parasites were estimated to be in the pupal stage, were put in the ship's ice-chamber as a last resource in the hope of extending the pupal stage until Fiji was reached. The average temperature of the ice-chamber appeared to be about 62° F. This method of treatment proved to be very successful, for, without a single exception, the twenty-five eggs all produced parasites on the day they were removed from the ice-chamber, or on the following day, after being subjected to a low temperature for nine days. These twenty-five adult parasites were landed in good condition in Fiji.

It was necessary for the ship and the parasites to be quarantined for smallpox on arrival in Fiji. Many difficulties arose from this, and in view of their short adult life and the impossibility of providing them with suitable host eggs on the small quarantine island of Nukulau, the twenty-five parasites were liberated there in the hope that they would find suitable eggs of their own accord. Although the number landed was so small, it would have been ample for breeding in captivity had a good supply of suitable host eggs been available, but it was doubtful whether such a small number of parasites could establish themselves in the field. Two or three species of Lycaenids and a great variety of small moths occur on Nukulau, and if the parasites discovered any of these it is possible that they may yet be recovered. No thorough search has yet been made for them.

This shipment served to show that the methods employed for breeding *T. nana* on board were practicable and that this and other similar parasites can easily be introduced into Fiji in the future if they are needed.

THE PREDACIOUS BEETLE, CALLIMERUS ARCUFER

Callimerus arcufer, Chapin (Plate XXXII, Figs. 5–8)

1. Description and Systematic Position

This Clerid beetle was described by Chapin [*] in 1919 from a female collected by Prof. C. F. Baker at Penang, Federated Malay States.

Chapin's description of the adult is as follows :—

> " Elongate, parallel, blue, marked with lines and patches of white scales. Head finely and quite densely punctured, rather different from the usual condition as found in this genus. Antennae short, reaching to the posterior border of the eyes, dark testaceous. Mouth parts piceous. Surface of head very sparsely clothed with scales. Thorax hardly dilated, anterior and posterior constrictions feeble, punctuation moderately coarse and quite sparse. There are four patches of scales, one on either side of the median line at both the anterior and posterior constrictions. Elytra coarsely and moderately densely punctured, the punctures not in rows. On the second quarter of the length there is a U of white scales common to the elytra. The upper ends of the figure are connected with the side margins by lines of scales. Just back of the U there is a transverse bar of scales and a second bar, somewhat wider than the first, is placed subapically. The under parts are finely and sparsely punctured, the lateral portions scaly. The anterior and middle femora are pale on basal half. The rest of the legs is dark. Posterior tibiae without subapical notch.
>
> " Length : 6 mm.
>
> " Male—unknown.
>
> " Female—terminal segments simple, unmodified.
>
> " Type—a female from Penang, Federated Malay States. C. F. Baker."

The male can be readily distinguished from the female by its denser white scaling on the anterior surface of the head. The posterior border of the penultimate ventral segment in the male is deeply emarginate. In other respects the sexes are similar.

2. Range

The species is recorded from the Federated Malay States and Sumatra.

3. Hosts

With such a generalised predator as *C. arcufer*, the term " host " is perhaps rather misleading, but we retain its use here for want of a better descriptive title for those insects on which it feeds.

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[*] *Proc. Biol. Soc. Washington*, **32**, 1919, pp. 225–234.

In addition to feeding on all stages of *Levuana iridescens,* adults and larval beetles have been fed on the following insects in captivity :—

Prodenia litura—eggs and larvae.
Plutella maculipennis—larvae and pupae.
Eublemma sp.—larvae and pupae.
Agonoxena argaula—larvae and prepupae.*
Tirathaba trichogramma—larvae.
Ptychomyia remota—larvae and pupae.

But with captivity feeding we obtained a more vigorous stock by feeding the beetles on *Levuana iridescens* than on any other of the above listed species.

When other food was scarce, the beetles fed readily on their own kind, adults, in particular, frequently eating their own eggs, often directly after depositing them.

In Malaya this beetle was first recorded as a predator on *Artona catoxantha*, but Gater (1926) has since found its larvae attacking the puparia of *Ptychomyia remota*.

This list shows that the beetle is not a very specialised predator ; and although its normal habitat, the coconut, may limit its attacks to insects that frequent that plant, there is good reason to think that it will attack almost any soft-bodied insects which feed in accessible places and which are sufficiently sluggish in their habits to allow of their capture.

We made no attempt to ascertain a further range of " hosts " in the laboratory. The insects listed above were tested either because of their comparative abundance around Suva, or because of their economic importance as coconut pests. The fact that the beetle was reared right through its early stages on *A. argaula* and *T. trichogramma* enhances its value as a predacious insect to the coconut growers in Fiji.

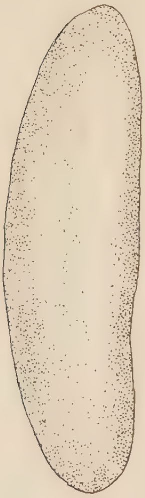


FIG. 116.—*Callimerus arcufer.*—Egg. × 55.

Aspidiotus destructor was tried as food, but the beetles would not feed on it.

4. Description of Early Stages

The Egg (Fig. 116).—The egg is pale yellow, glossy when first laid, becoming slightly crinkled before hatching.

Chorion, thin, colourless and unsculptured.

Sub-elliptical in shape ; usually somewhat curved about the longitudinal axis.

Average length . . . . 1·6 mm.
,, width . . . . 0·40 mm.

Larvae.—There are normally three larval stages.

A description of the mature larva has been made by Dr. A. G. Böving (*Proc. Ent. Soc. Wash.*, **30**, no. 6, June 1928) and need not be repeated here.

---

* The larvae of this moth are too active and its pupae too heavily chitinised to allow the smaller beetle larvae to feed on them. The prepupal stage is the only one attacked by such beetles under natural conditions.

First Instar.—When newly hatched, the first-stage larva is pale, except for the eyes and terminal segment which are black and the mouth parts which are brown (Fig. 117).

For the first two days after hatching there is little change except an increase in length, but later in the instar, the larvae become more differentiated in colour (see Fig. 118).

In the mid-dorsal line extending from the prothorax to the seventh abdominal segment there is a darkened area. There is a small dark circular patch on either side of the mid-dorsal line on the prothorax and eighth abdominal segment. The entire dorsal aspect of the metathorax and the second, fourth, sixth and seventh abdominal segments is decidedly darker in colour than that of the remaining (except the caudal) segments. There is too much variety in the size and colour of the first-instar larvae to allow of a concise description being made. Later in the instar the larvae are pale brown with the darker integument of the five body segments referred to above causing a banded appearance which persists throughout the later instars. The larva is hairy and slightly flattened dorso-ventrally.

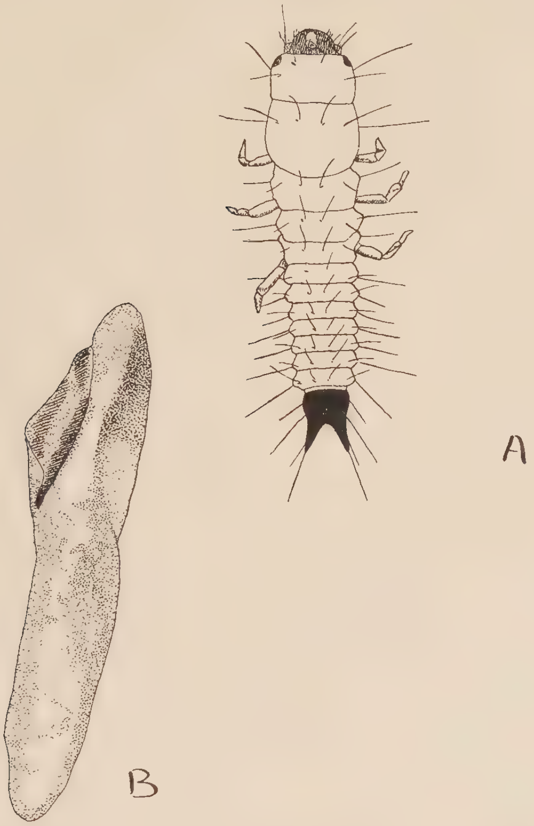


FIG. 117.—*Callimerus arcufer*, Chap.—A. Newly hatched larva. B. Egg showing dehiscence after hatching. Both × 55.

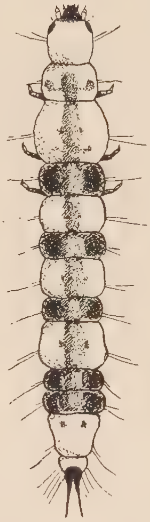


FIG. 118.—*Callimerus arcufer*, Chap.—First-stage larva just prior to the first moult. × 20.

Second Instar.—This stage is easily distinguished from the previous one by the appearance of a pair of dark, thickly chitinised " plates " on the dorsum of the prothorax. These two plates are separated narrowly mid-dorsally. They are present in the third instar, but are never developed until after the first moult.

As in the previous instar, there is a considerable range of colour displayed by different individuals. A change in colour usually takes place sometimes during this instar; but it is occasionally delayed until after the second ecdysis. From the pale brown typical of the first instar the colour changes to blue or green, with the five transverse bands now becoming almost black.

The urogomphi, which form a two-pronged " tail " projecting posteriorly from the ninth abdominal segment, are longer in this than in the previous instar. The head is pale brown. Dorso-ventral flattening is still a feature of the head and prothorax and to a less extent of the trunk. When full fed, the maximum width seems to be at the fifth abdominal segment, whence the body tapers gradually anteriorly and more abruptly posteriorly.

The majority of the late second-instar larvae are blue coloured. The green-coloured type described by Gater was not so commonly found with us. Doubtless food is the deciding factor in colour determination—since larvae fed on the green caterpillars of *Eublemma* and *Plutella* are distinctly green, whilst those fed on *Levuana* are blue.

Third Instar.—In the third stage the head capsule becomes dark brown, highly chitinised and considerably broader than in the second stage.

The colouring of the third-stage larva is briefly described by Gater (1926). We have nothing to add to his description in this summary account, except that in most of our specimens, the bulk of which were fed on *Levuana*, blue was the predominant colour rather than green.

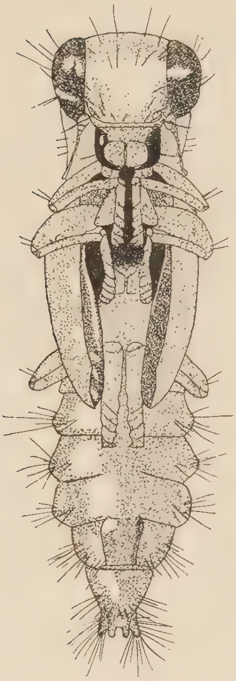


FIG. 119. — *Callimerus arcufer*, Chap.—Pupa, × 20. Ventral view.

When full grown, the larva averages 10 mm. in length, but individuals as long as 11·5 mm. have occasionally been seen.

The Prepupal Stage.—The dorso-ventral flattening becomes obliterated by the contraction of the body. The colour remains the same, but less vivid than at the close of the feeding period.

The cocoon is described by Gater (1926). We can add to his description the fact that the structure and shape of the cocoon vary according to the position selected for pupation. There are two main types of cocoon. When a beetle chooses to construct its cocoon between two closely apposed surfaces, it uses these surfaces to form the roof and floor of the pupal cell, fixing them together with a double row of silken threads which forms the side walls of the oval-shaped cell. When, on the other hand, only one surface is available on which to pupate, the cocoon is spun right over the body of the larva just as in *Levuana*.

The Pupa (Fig. 119).—Hair tufts are present on the abdominal segments as in the larva. The head and thorax are sparsely clothed with rather fine hairs arising singly or in pairs.

The cerci are very short and do not differ in colour from the remainder of the body, which is predominantly pale blue.

When newly formed, the pupa is very pale in colour and the appendages are white. Towards maturity the colouring of the adult beetle becomes more pronounced. There is much variety in size, but the average length is 7·5 mm.

5. LIFE-HISTORY

The duration of the early stages varies within fairly wide limits according to the temperature and food supply. Larvae remained alive for several days without food, in the breeding tubes.

There is a considerable lapse of time, sometimes as much as six weeks, between emergence of the adult and commencement of oviposition; thus the total life-cycle varies from eight to thirteen weeks, whereas the early stages are passed through in from six to eight weeks.

Our first set of life-history observations was made during the months December to March 1925–26; but we think by comparison with other records made from June to August 1926 that these were not typical for all seasons of the year.

The following table, wherein are set out the maxima, minima, and mean periods for the several stages, is therefore based on the combined data from the two sets of records. The figures given, which are days, are therefore probably average for the development of the beetle in Fiji at all seasons.

When an abundant food supply was provided, adults were kept alive for just over five months in the breeding tubes.

TABLE SHOWING THE LIFE-HISTORY OF *CALLIMERUS ARCUFER*.

		MAXIMUM.	MINIMUM.	MEAN.
		Days.	Days.	Days.
Incubation		16	6	8·5
First instar		19	5	10·9
Second instar		12	8	10·1
Third instar *		13	6	8·8
Prepupal period		9	6	7·0
Pupal period		14	8	10·6
Total period of early stages		54	40†	49·0
Adult remains in cell		5	2	3·3
Oviposition starts		43	16	24·4
Total life-cycle ‡		102	58	76·7
Adult life in captivity	Female	154	—	—
	Male	156	—	—

* Exclusive of the period spent within cocoon (prepupal stage).

† This figure was obtained from an individual which pupated at the second ecdysis.

‡ These figures are based on the sum of figures quoted in three preceding columns: not on individual records.

6. Omission of an Instar

During the life-history studies on *Callimerus arcufer* it was found that perfectly normal second-stage larvae not infrequently assumed a prepupal condition and subsequently pupated without first passing through a third-larval instar. Sometimes such individuals pupated without constructing any cocoon ; but the majority of them made a cocoon which was identical with that formed by third-instar larvae.

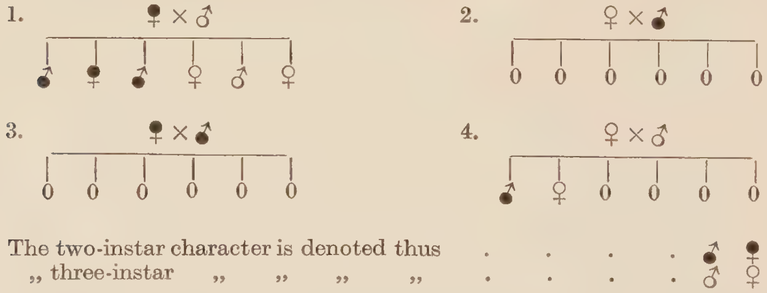
Dr. Chapin, who has studied numerous Clerid larvae, informed us that he has never come across any instance of the omission of an instar during his studies of these insects. We, therefore, endeavoured to determine experimentally the cause of this unusual phenomenon.

Food was not the deciding factor—since both the two or three instar type of individuals occurred with identical conditions of feeding during their previous development. Neither was it a matter of sex, since approximately equal numbers of males and females emerged from individual pupae that displayed this two-instar larval development. Furthermore, the sexes are produced in approximately equal numbers in this species, whereas the percentage of three-instar to two-instar individuals was at least 5 : 1.

It was thought that possibly the two-instar type of development might be caused by some inherited factor, so that the progeny of abnormal individuals would themselves display the same peculiarity. We started experiments to determine if this proved true ; but owing to the length of the generation and the lack of time at headquarters necessary to give the experiments the necessary detailed attention, we were unable to bring the matter to any conclusion. But we did show, by studying a selection of the progeny of four crosses, that in the F_1 generation there was no segregation into a simple Mendelian ratio, and that the peculiarity was not inherited in the first generation by all, if any, of the progeny.

Callimerus arcufer

Table showing Progeny of F_1 Generation derived from Four Separate Crosses made between Two- and Three-instar Individuals


1.
♀ × ♂
♂ ♀ ♂ ♀ ♂ ♀
2.
♀ × ♂
0 0 0 0 0 0
3.
♀ × ♂
0 0 0 0 0 0
4.
♀ × ♂
♂ ♀ 0 0 0 0
The two-instar character is denoted thus . . . . ♂ ♀
,, three-instar ,, ,, ,, ,, ... ♂ ♀

N.B.—The sex of the majority of individuals of the F_1 generation was not determined, their development being studied only sufficiently long to determine whether or not they had a two- or three-instar larval life.

The above table gives the results obtained by our preliminary experiments. For reasons stated above we were unable to devote the necessary time to studying a long series of individuals, the results were therefore based on six eggs, in each case selected at random at intervals during the life of the parents' crosses.

7. HABITS AND BEHAVIOUR

C. arcufer is a predatory insect. It will not survive solely on a scavenging diet, but must have living insect food at intervals, although in the larval stage, more especially, it often feeds temporarily as a scavenger on the carcases of previously killed insects.

The adult beetle is the most voracious in its feeding habits, a single adult sometimes killing five mature *Levuana* larvae in the course of a day's feeding. Its method of feeding is rather interesting. It generally approaches its prey from behind, grasps it with its powerful mandibles, and often severs the body almost completely in two at the first bite. The beetle then retreats backwards, dragging with it a stream of the fluids which have issued from the wounded host. The mandibles chew at this semi-liquid substance, and sometimes remain motionless for a minute or two immersed in the fluid as if the beetle was imbibing by suction the blood of its prey ; structurally, however, there seems to be no evidence to support the view that the suctorial method of feeding is adopted by this insect, although there is a tendency amongst certain families of beetles with mandibulate mouth parts to subsist solely on fluid food.

After the completion of this first assault, the beetle reapproaches the now lifeless host, bites it again, and continues imbibing the fluid until the carcase is almost dry. At this stage the beetle will often abandon the original prey and go in search of another living caterpillar. But if the latter is unobtainable, it will continue to chew at the original prey until nothing is left but the skin and head capsule.

The larva adopts a somewhat different manner of feeding. The mandibles are much smaller than those of the adult, and the method of killing the host is usually to bite through the thin ventral integument so as to cause bleeding. Not infrequently the smaller beetle larvae drown in the drop of blood which issues from the wound. On two occasions we found first-instar Clerids with the head fixed into the integumental funnel of a parasitised *Levuana* caterpillar. Death in this case must have been due to the beetle larva being unable to withdraw from the funnel after becoming swollen with feeding. Being holopneustic, the larva would not have been asphyxiated in this instance. The larvae are slow feeders, and even when full grown seldom require more than one full-sized *Levuana* caterpillar to satisfy their daily appetite.

The adults are diurnal in their habits and rest at night, but the larvae feed during the night when kept in captivity. The larvae do not seem to start feeding until nearly two days after hatching ; except for the occasional consumption of the egg-shell immediately after hatching. Both larvae and adults are very active insects when disturbed : the latter take to the wing fairly readily.

In captivity adults frequently underwent a series of violent "spasms," lying on the back and moving the legs violently, until finally they would assume a motionless attitude apparently dead. This semblance of death—if such it was—was not apparently induced by any external stimulus ; it can therefore hardly have any protective value, as in the case of weevils, etc. On more than one occasion we have been deceived into believing that an adult *Callimerus* was dead, only to find the same beetle very much alive on the following day.

The larvae have two distinct methods of locomotion. When they are leisurely surveying their feeding ground, or crawling over a treacherous surface, they use the modified tenth abdominal segment as a locomotory clasper with which they can anchor the body posteriorly and explore what lies ahead of them by moving the front part from side to side. Progress by this means resembles somewhat that employed by a Geometrid larva.

The more normal method of progress, and that employed when the larvae are disturbed, is effected by crawling with the thoracic legs only. By this means larvae are able to crawl very rapidly, and the legs move so quickly that the whole insect has the appearance of gliding over a surface.

In Malaya the habitat of this beetle seems to be the coconut palm and its principal food *A. catoxantha.* The dorso-ventral flattening of the anterior part of the larva suggests an adaptation for opening the lid of the cocoons and gaining access to the host pupae. The latter seem to provide the most frequent source of food, the larval beetles using the host cocoon as a retreat beneath which they shelter. They often complete their development and construct their own cocoons under those of the Zygaenid host. Similar habits are displayed in Fiji with the allied host *Levuana.*

Adults, on the other hand, feed more on the larvae and seldom break open the cocoons.

Mating is a fairly lengthy process, although we have not made records of its exact duration. A female usually mates several times during its life. We have evidence to show that the supply of sperm received during the first act of copulation does not always last until the female has laid all her eggs. In one instance a fertilised female kept alone in a tube started ovipositing on the twenty-first day after emergence ; she laid 163 fertile eggs during the succeeding fourteen weeks and then commenced to lay infertile eggs, depositing ten in the course of so many days. Another male was therefore placed in the tube, mating took place, and the female then laid another thirty fertile eggs before dying.

In another instance a male and female were observed in copula on seven occasions during an adult life of five months. We mated one male with no less than eight different females. We have not observed mating sooner than a week after emergence from the cocoon.

Oviposition usually starts two to three weeks after emergence irrespective of mating because females lay infertile as readily as fertile eggs. When infertile eggs are laid, they are frequently eaten by the female that deposited them.

The ovipositor is long and flexible, and almost entirely withdrawn into the body when not in use.

When we kept *Callimerus* in large breeding cages containing small palms loaded with host larvae as food, we found eggs laid beneath the pupae of the host; and this is almost certainly the typical position in which they are deposited in the field, the ovipositor being admirably adapted for probing beneath the edge of the host cocoon.

In captivity the adults laid readily in cotton wool plugs, but the majority of eggs laid in that position were inserted well beneath the surface of the plug.

The average number of eggs laid each day by one beetle worked out at about one. But from three to six eggs in one day were commonly obtained from certain individuals and as many as eleven eggs were laid in a day in one instance. The largest number of eggs obtained from one beetle was 203, but the majority of females which laid at all deposited between fifty and a hundred eggs.

8. Introduction to Fiji

This species was introduced to Fiji with *Ptychomyia remota* in August 1925. Less than a hundred individuals (adults and larvae) were removed from the imported breeding cages during the six weeks subsequent to landing the stock at Suva. These few beetles formed the basis of our laboratory breeding stock. The species must have bred in the cages during the journey from Malaya to Fiji, because several small larvae were removed on arrival in Suva, so that hopes were entertained of breeding up the species in captivity for colonisation throughout the group.

Nothing was known of the eggs or pupae or of the duration of the immature stages at the time of introduction from Malaya, so that it was considered advisable to liberate a percentage of the landed stock before risking loss of the entire stock by experimental captivity breeding.

Adults kept in a glass tube plugged with cotton wool were seen to oviposit in the plug, and this gave a clue as to their requirements for oviposition as well as material for study of the egg stage and life-history.

Shortly afterwards pupal cells were found amongst the fibre at the base of the coconut leaves; so that it was then possible to provide the necessary conditions for breeding in captivity.

9. Breeding in Captivity

The species would not breed quickly in a large cage, so we evolved the following method, which proved quite satisfactory provided that an abundant food supply was available.

The adults were kept in glass tubes plugged with cotton wool stained black so as to facilitate recovery of the pale-coloured eggs.

A newly emerged male and female were put in each tube and left together for ten days, or until mating was observed.

Oviposition commenced about sixteen days after adult emergence, the eggs being laid in the cotton wool.

Each adult was provisioned with five *Levuana* larvae every day. It was found inadvisable to use mature caterpillars as food, because they often started to pupate against the walls of the tube and induce oviposition by the beetle beneath their cocoons, instead of the more easily removed cotton plug.

Adult beetles have no hesitation in eating their own eggs, especially if food is not forthcoming, so that the success of breeding this species in captivity depends on separation of the various individuals as well as provision of a plentiful food supply for the adults.

The eggs were removed and counted each day and transferred to other tubes. When the eggs hatched, the young larvae were transferred on a fine brush to separate small glass tubes plugged very tightly with cotton wool.

One host caterpillar or pupa per tube was found sufficient to feed the first-stage beetles for a few days ; it was important, however, to see that the larvae discovered the food proffered, otherwise they would often take up a position against the cotton plug until they died of starvation.

The food was renewed in the larval tubes as occasion demanded ; the larvae can, however, survive a fast of several days, so that the larval tubes did not require such regular attention as did those containing the adults.

After larvae had spun their cocoons, no further attention was required until adult emergence from the cell—seventeen days later.

It was found necessary to keep the breeding tubes perfectly dry, the beetles deriving all the moisture they required from the juices of their prey.

By numbering the breeding tubes, we were able to keep a check on the eggs laid by each female, and to study the life-history in detail.

The drawback to this method of breeding as a routine was the length of time required for its efficient execution. A large and constant supply of Lepidopterous larvae was necessary for a rapid increase of our stock, and when *Levuana* became scarce around Suva about the middle of 1926, it was a matter of some difficulty to procure sufficient food to increase our stock of beetles.

As soon as the life-history and habits of the species had been studied the work of breeding the stock for colonies was left in the hands of native assistants, who although able to devote their entire time to the task and fully cognisant with the routine methods, were unable to make rapid increase in the stock, largely through inability to procure sufficient food.

Levuana had in the meantime become reduced so completely by *P. remota* alone that it was decided to abandon the laboratory breeding, after the liberation of altogether about 1,000 beetles.

With plentiful food available in June and July 1926 (largely the larvae of *Eublemma* sp. from the rain-tree *Albizzia lebbek*), we were able to increase our stock of beetles from thirty-five to 239 in six weeks, this being effected with a breeding stock of only ten females.

10. Liberation of Colonies

Owing to the hardiness of the beetle and the abundance of food during the first few months after its introduction to Fiji, it was considered that colonies of fifty individuals would be adequate.

Had we then known that *Callimerus* was not going to become quickly established on *Levuana*, but would be dependent on other hosts, it would probably have expedited rapid establishment of the beetle if the strength of each colony had been increased to a hundred or more individuals.

The list of colonies liberated is given in tabular form as follows :—

Colonies of *Callimerus arcuffer* liberated in *Fiji*, 1925–1928.

Date.	Number in colony.	Locality.
18.8.25	29	Nanuku—Ra
8.9.25	33	Nanuku—Ra
2.2.26	50	Cawatara—Ovalau
2.2.26	50	Vuma—Ovalau
17.2.26	50	Rukua—Beqa
5.3.26	40	Rukuruku—Ovalau
5.4.26	48	Bau Road—Rewa
24.4.26	50	Nausori—Rewa
19.7.26	13	Vutia—Rewa
9.9.26	30	Leleuvia
14.9.26	25	Suva
18.9.26	61	Nasese—Suva
18.10.26	50	Nasese—Suva
26.10.26	23	Nanukuloa—Ra
11.11.26	50	Makuluva
12.11.26	50	Leleuvia
13.11.26	50	Ulibau—Moturiki
16.11.26	53	Yanucalevu
24.9.27	169	Savu Savu—Vanualevu
16.11.27	105	Mua—Taveuni
3.3.28	80	Wainibokasi—Rewa
Total . .	1109 in 21 colonies.	

When possible, trees heavily infested with *Levuana* were selected as sites for colony liberation, the larvae or adults being placed amongst the leaf bases or " vulu " on pupal masses of the moth.

11. Part played in Control of Levuana

We have not recovered *Callimerus arcufer* in the field,* and we are certain that it played no direct part in the control of the moth effected during the latter part of 1926.

In November of 1926 a colony of larvae was liberated on Makuluva where deal conditions obtained for its establishment. *Levuana* was abundant on that island for the subsequent twelve months, and if the beetle had bred on *Levuana* with any degree of rapidity, we should certainly have recovered it during 1927. But no sign of the insect was met with.

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* In two colony sites on the Lower Rewa flats a pupa and adult were found on the trees on which larvae had been liberated less than a month beforehand. After this, no further recovery was made in the localities concerned.

Since the beetle has been reared on such generally abundant species as *Agonoxena argaula* and *Tirathaba trichogramma*, and seems fairly catholic in its tastes, it is hoped that it may become established in the group and help in the control of the two lesser coconut pests just referred to.

To this end, a strong colony has been liberated on each of the two most important copra-producing islands—Vanualevu and Taveuni.

In captivity we have obtained the following data regarding the power of the beetle as a predator on *Levuana* :—

	No. of host larvae * killed. Max.	Min.	Mean.
During first instar	4	1	3·0
,, second instar	6	1	3·7
,, third instar	5	1	3·3

Each beetle larva was therefore responsible for the death of some ten *Levuana* larvae * during the course of its development.

The adults ate more than the larvae, and as they will feed on the leaves on all stages of the moth, they are more useful as predators than the larvae.

Adults ate on an average 2·5 *Levuana* * per day ; whereas the larval rate of feeding was only a tenth of this figure. The largest number of larvae killed by an adult in one day was five. This number would be increased considerably by feeding with small larvae only.

If this species becomes established in Fiji and selects *Levuana* for its principal food, it will certainly help in maintaining control of the moth in small local infestations where the parasitism by the Tachinid is apt to become low. But its killing powers and rapidity of increase fall far short of that of the predacious bugs that attack *Levuana ;* and the fact that adults and larvae of the Clerid will feed indiscriminately on parasitised and unparasitised *Levuana* detracts somewhat from the value of the species as a *Levuana* control agent.

12. Natural Enemies in Fiji

It seems possible that *Callimerus* is being prevented from increasing rapidly in the field by some controlling agent, but we have not been able to study this matter carefully.

The small predacious ant *Tetramorium guineense* attacked first-stage *Callimerus* larvae immediately they were liberated at Rukuruku on Ovalau. This is the only instance of ant attack that we have seen, but owing to the abundance of this ant it is possible that it has been responsible for the failure of rapid establishment of our colonies.

On Leleuvia a small centipede attacked a mature *Callimerus* larva while it was crawling up the trunk of a coconut tree after liberation. The centipede bit the Clerid several times, but apparently the cuticle of the latter was sufficiently thick to prevent penetration of the mandibles of its assailant. In any case the centipede soon abandoned further efforts to attack the beetle, and the latter resumed its course apparently unaffected.

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* Either mature larvae or pupae.

The only other instance met with of attack by another insect is a special case which can scarcely occur in natural surroundings. A *Ptychomyia remota* fly oviposited on a third-stage *Callimerus* larva inside a breeding tube ; and the Tachinid maggot entered and killed the beetle and in due course a fly matured. It seems exceedingly unlikely that this can ever occur in the field.

Gater makes no mention of any insect attacking *Callimerus* in Malaya.

The location of the bulk of the host (*Levuana*) pupae on the leaf bases instead of on the leaves (*Artona*) may have some influence on the development of the larvae. We know that excessive moisture is fatal to larvae contained in tubes, and the pupal masses of *Levuana* at the angles between the trunk and base of the leaves would be more likely to collect moisture than the isolated cocoons of *Artona* situated on the sheltered under surface of the leaves.

AN ANNOTATED LIST OF THE MORE IMPORTANT LITERATURE ON LEVUANA IRIDESCENS PUBLISHED IN FIJI

Carment, A. G.			
	1921	Agric. Circ., Vol. 2, No. 2, p. 20.	Reference to a parasitic fungus from Malaya.
	1921	Agric. Circ., Vol. 2, No. 2, p. 85.	Report on experiments with an indigenous fungus.
	1921	Agric. Circ., Vol. 2, No. 5, p. 114.	*Pediculoides ventricosus* found in pupal masses.
	1922	D. of A., Ann. Rep., 1921 (C.P. 56), p. 8.	Note on parasitic fungi.
Despeissis, A.			
	1924	D. of A., Ann. Rep., 1923 (C.P. 53), p. 3.	Reference to the setting up of a Levuana Control Committee and to arrangements made for financing this project.
	1924	Agric. Circ., Vol. 5, No. 1, pp. 1–14.	Includes a reprint of an earlier paper on *Levuana* by Knowles, and in this reprint notes are added by A. M. Lea and H. W. Simmonds. Illustrated.
	1925	D. of A., Ann. Rep., 1924 (C.P. 44), p. 2.	Gives a brief account of A. M. Lea's mission to Malaya, Java, and Queensland.
Jepson, F. P.			
	1911	*Report on Economic Entomology* (C.P. 25).	At p. 35 *et seq.* there is a full account and description of the *Levuana* moth. At pp. 9, 10, 71 and 77 are short references to this insect.
	1915	D. of A., Ann. Rep., 1914 (C.P. 24), p. 20.	Notes on control by the use of lead arsenate and on the introduction of fungus *Botrytis necans* from the F.M.S.
	1915	D. of A., pamphlet No. 16.	Notes for the information of planters.
	1916	D. of A., Ann. Rep., 1915 (C.P. 29), p. 17.	Gives some records of early breeding experiments.
	1916	D. of A., pamphlet No. 25.	Report on visit to Rewa Plantations (p. 3) mentions the occurrence of *Levuana.*
	1917	D. of A., Ann. Rep., 1916 (C.P. 107), pp. 17 and 22.	Notes on the occurrence of *Levuana* on ornamental palms and on observations and experiments with *Canthecona cyanacantha.*
Knowles, C. H.			
	1906	D. of A., Ann. Rep., 1905 (C.P. 23), p. 7.	*Levuana* observation at Caboni and reference to description by Hampson.
	1907	D. of A., Ann. Rep., 1906 (C.P. 13), p. 7.	Reference to description of the occurrence of *Levuana* during the year and to its being preyed upon by a large blue Pentatomid bug.

1909	D. of A., Ann. Rep., 1908, (C.P. 27), p. 23.	Notes on occurrence and on the finding of various stages in the field.
1916	D. of A., Ann. Rep., 1915 (C.P. 29), pp. 13 and 31.	Brief notes on coconuts at Nasinu and on *Botrytis necans*.
1916	*Laucala Coconut Experiments* (C.P. 34).	Spraying experiments with arsenate of lead.
1917	*Laucala Coconut Experiments* (C.P. 84), pp. 1, 3, 4, and 5.	Notes on the occurrence of the moth and on the effect of spraying and of smoking.
1918	D. of A., Ann. Rep., 1917 (C.P. 60), pp. 4 and 9.	Notes on occurrence and on the death of some trees also on *Cantheconа*.
1919	D. of A., Ann. Rep., 1918 (C.P. 32), p. 12.	A brief reference to occurrence in the dry zone and to the presence of *Polistes* and other predators.
1919	D. of A., Bull. 12, entitled, *A Small Leaf Moth on Coconuts in Fiji*.	A useful publication giving a summary of all the information on *Levuana* down to date together with illustrations and a bibliography.
1920	D. of A., Ann. Rep., 1919 (C.P. 65), p. 6.	Mentions occurrence at Nasinu.
1921	D. of A., Ann. Rep., 1920 (C.P. 39), p. 8.	Mentions uneven distribution and reference to a Braconid parasite on a related insect in the F.M.S.
Lea, A. M.		
1924	Agric. Circ., Vol. 5, No. 1, Bull. 15, pp. 48, 49, and 50.	This is a reprint of Knowles' Bull. 12 in which a few annotations are made by A. M. Lea.
Lees, H. B.		
1922	Agric. Circ., Vol. 4, No. 4, p. 54.	Information to planters regarding the *Levuana* insect.
Simmonds, H. W.		
1920	Agric. Circ., Vol. 1, No. 7, p. 138.	Refers to an astringent variety of coconut in Tahiti and suggests that it might not be attacked by *Levuana*.
1921	Agric. Circ., Vol. 2, No. 2, p. 19.	The " Oviri " or astringent coconut planted.
1921	Agric. Circ., Vol. 2, No. 4, p. 84.	Brief notes on history, occurrence in Suva, and on the non-immunity of the " Oviri " nut.
1921	Agric. Circ., Vol. 2, No. 7, pp. 102, 103, and 121.	Brief notes.
1922	D. of A., Ann. Rep., 1921 (C.P. 55), p. 6.	Summary of the points noted in the other literature of 1921.
1922	Agric. Circ., Vol. 3, No. 3, p. 44.	Short discussion on occurrence in wet and dry zones. Reports feeding on bananas.
1922	Agric. Circ., Vol. 4, No. 4, pp. 52 and 53.	Brief historical summary and with an account of the spread of *Levuana* to Lomaiviti.
1923	D. of A., Ann. Rep., 1922 (C.P. 46), pp. 3 and 4.	Brief reference to the spread of the insect to Caqalai and Moturiki and to the irregular occurrence of *Levuana* in the dry zone.
1924	D. of A., Ann. Rep., 1923 (C.P. 53), p. 8.	States that *Levuana* is not in island groups to the north-west of Fiji. Brief reference to the spread of *Levuana* to Ovalau and Leleuvia.
1924	Agric. Circ., Vol. 5, No. 1, Bull. 15, pp. 52 and 75.	In the form of annotations gives a few notes and refers to false reports on occurrence of the insect on Vanualevu and Kadavu,

1924	*Mission to New Guinea, Bismarcks, Solomons and New Hebrides* (C.P. 2), pp. 2, 5, 9, 10 and 11.	Reports finding no related Zygaenids in territory visited. Gives short résumé on position in Fiji.
1925	*Pests and Diseases of the Coconut Palm,* D. of A., Bull. 16, pp. 14 and 15.	Gives brief description of the pest for the benefit of the planters. Nicely illustrated.
1925	Agric. Circ., Vol. 5, No. 2, pp. 88 and 103.	Refers to suggestion to introduce insectivorous bats and to legislation regarding cutter inspection.
1926	D. of A., Ann. Rep., 1925 (C.P. 36), p. 8.	Notes on occurrence during 1924.
TOTHILL, J. D.		
1925	Agric. Circ., Vol. 5, No. 2, pp. 83, 84, 85.	Policy of reorganised campaign outlined.
1925	Director's Report (C.P. 20).	Progress of campaign to July 1925.
1925	Director's Report (C.P. 71).	Progress of campaign to December 1925.
1926	D. of A., Ann. Rep., 1925 (C.P. 36), p. 3.	Reference to literature for the year dealing with the campaign.
1926	Director's Report (C.P. 18).	Progress of campaign to May 1926, gives in tabulated form a list of the *Ptychomyia* colonies liberated.
1926	Director's Report (C.P. 90).	Progress of campaign to November 1926.
WRIGHT, C. H.		
1920	D. of A., Ann. Rep., 1919 (C.P. 65), p. 13.	Notes on the occurrence of *Levuana* at Suva and a note on the occurrence of *Canthecona.*

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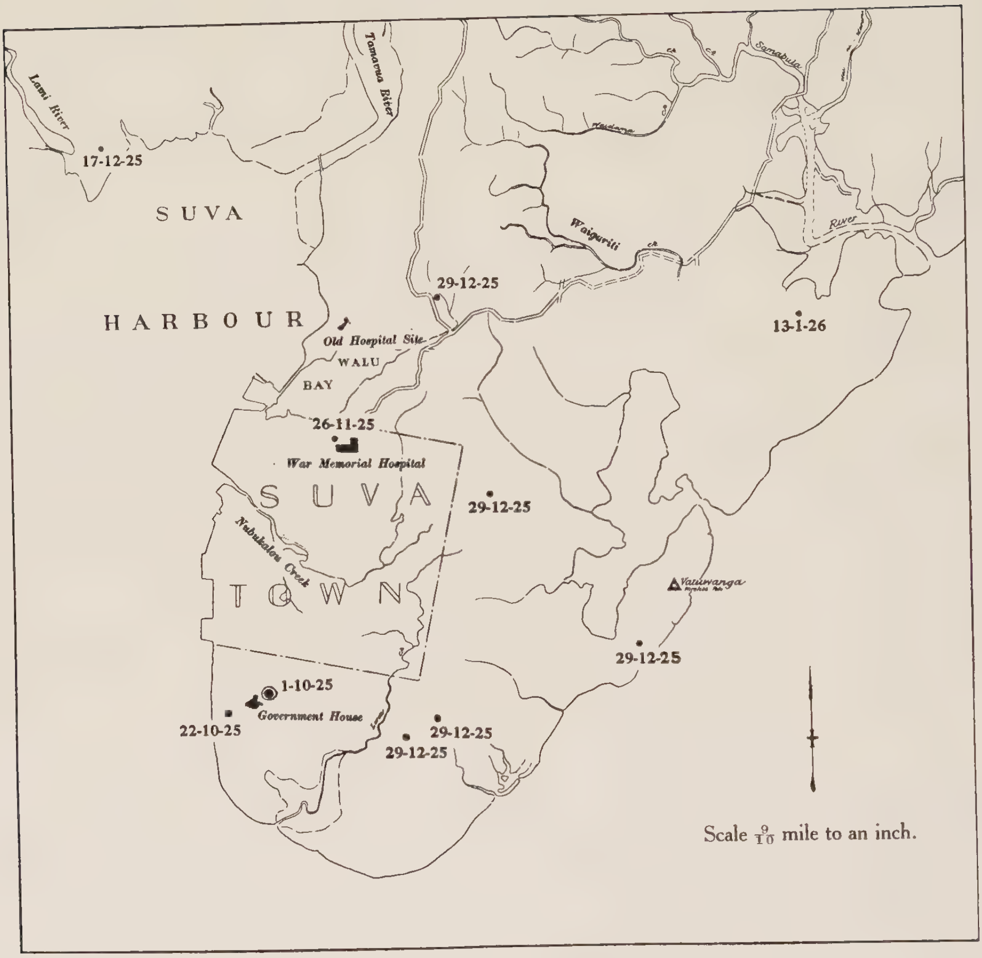
PLATE VIII


Lami River
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Waidanu
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River
29-12-25
13-1-26
Old Hospital Site
WALU
BAY
26-11-25
War Memorial Hospital
SUVA
TOWN
Nubukalou Creek
29-12-25
Vatuwanga
29-12-25
1-10-25
Government House
22-10-25
29-12-25
29-12-25

Scale $\frac{9}{10}$ mile to an inch.

PLATE VIII

Map of Suva and neighbourhood showing the early spread of *Ptychomyia remota*, Aldr., from the central insectary colony.

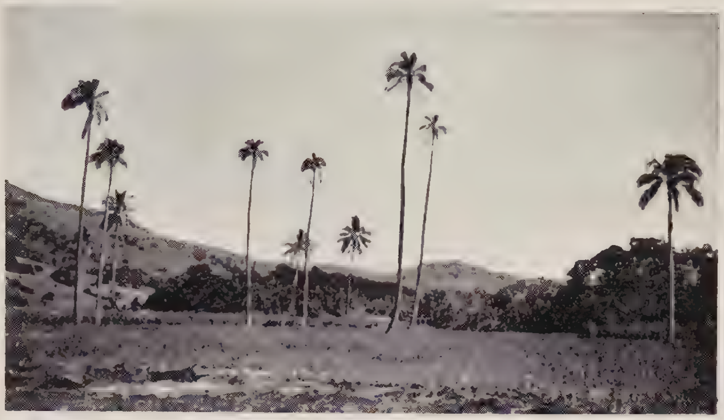
PLATE IX

SEVERE INJURY CAUSED BY *LEVUANA*

A. Old trees in swampy soil gradually dying from the effects of repeated attacks of *Levuana*. Manuku, Ra, vi/25.

B. A typical country scene in Ovalau towards the end of an outbreak of *Levuana*. Behind Nacombo in xi/25.

C. Part of Naigani island at the concluding stages of the 1925 outbreak. Except for two trees in the right-hand foreground, every tree shows almost complete defoliation. Such an attack as this leaves trunk constrictions on most of the trees. Naigani, xi/25.



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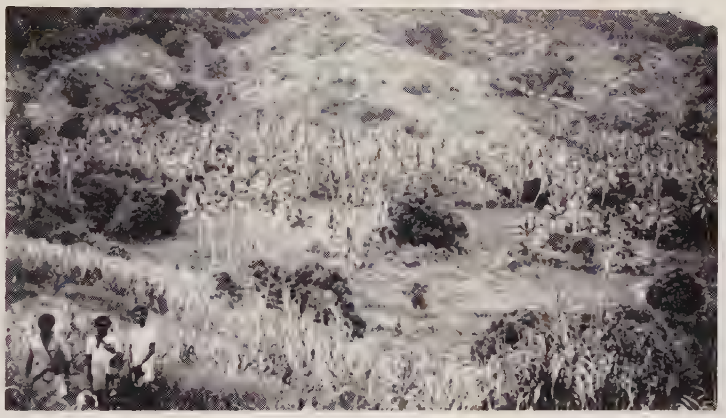

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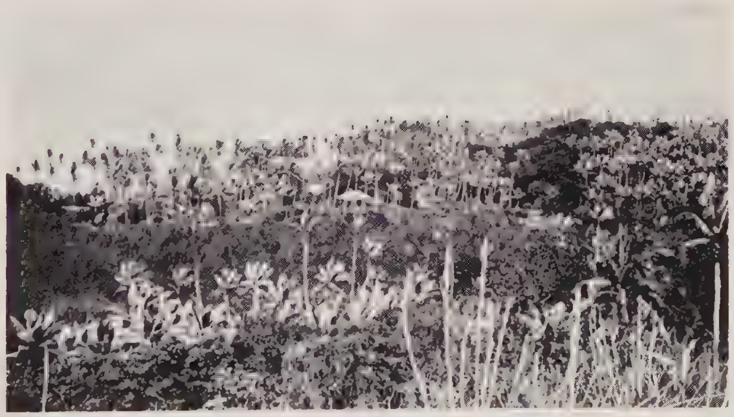

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PLATE X

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PLATE X

THE EFFECT OF *P. REMOTA*

A. Recovery of trees on Ovalau after the establishment of *P. remota*. The upper leaves are all entirely green and the lower ones all white or grey. On the coast road north of Levuka, ix/26.

B. Conditions similar to those in A at Vuma, Ovalau, ix/26.

C. *P. remota* became so numerous at Suva that it became very difficult to obtain *Levuana* larvae for feeding to the predacious beetle *Callimerus*. A cage was therefore built over a small coconut tree to screen out the fly.

PLATE XI

INJURY CAUSED BY *LEVUANA*

A. Contrast in appearance between a completely defoliated leaf and a healthy green one. Makuluva island, xii/27.

B. A completely defoliated tree. All the leaves on this particular tree were brown and riddled with feeding scars when the photo was taken. They have not yet begun to whiten and are therefore not conspicuous in the photo, but the crinkled appearance of the leaflets can be made out in places. Lovoni, iv/27.

C. Old tree in Government House Domain, Suva, showing marked trunk constriction two-thirds of the way up the trunk. This indicates a former *Levuana* defoliation.

PLATE XI

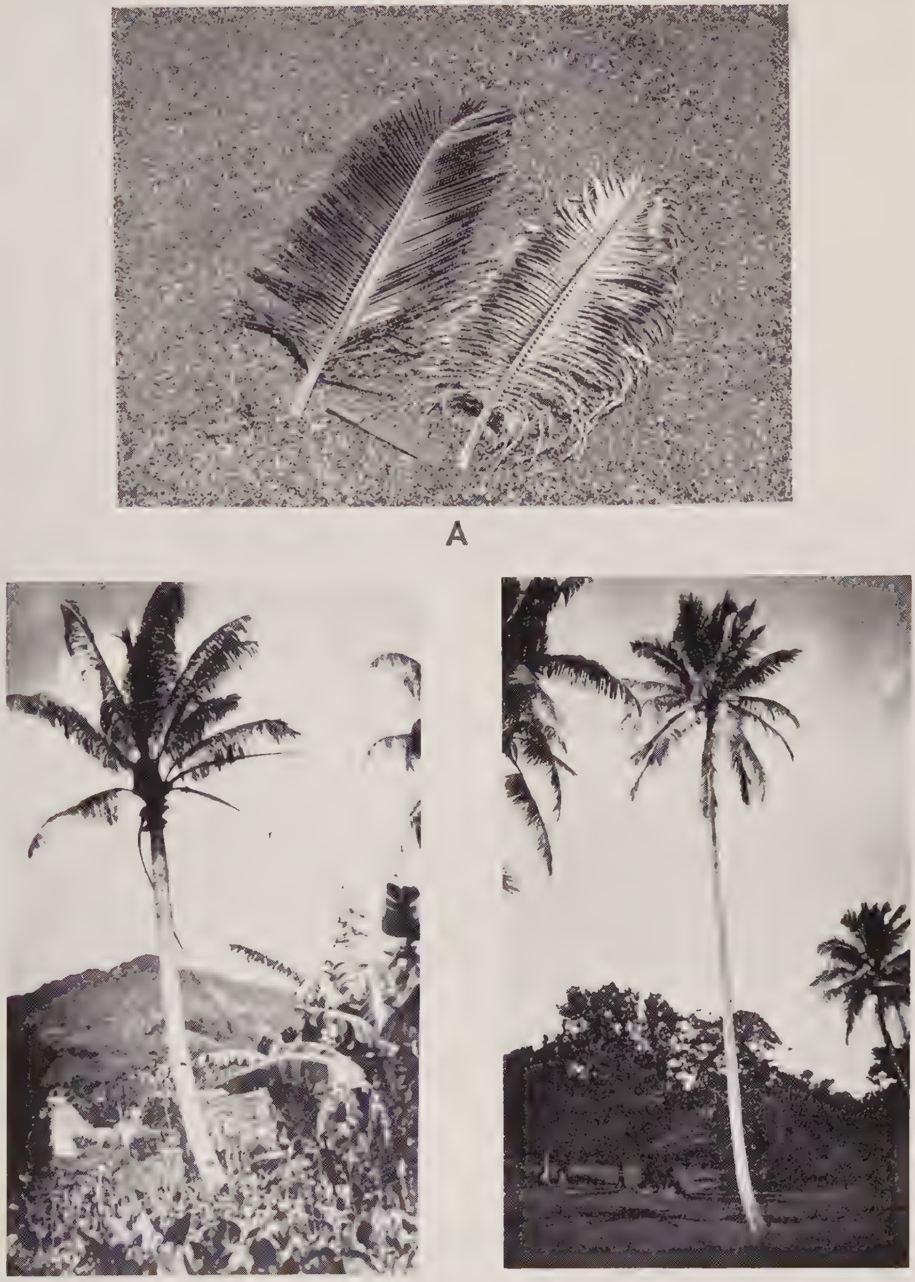

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PLATE XII

A

B

C

PLATE XII

TYPES OF *LEVUANA* INJURY

A. The two leaves shown in A of Plate XI. On the damaged leaf the leaflets curl over at the tips.

B. Top part of an old tree in Government House Domain showing the much-constricted trunk below the crown. The tree was severely attacked by *Levuana* two or three years previous to the date of photograph.

C. Trees dead and dying from the combined effect of *Levuana* and swampy soil. Viesoto (Ovalau), iii/26.

PLATE XIII

A. The range of normal flight of *Levuana* is restricted. The trees in the foreground are on the island of Wakaya which *Levuana* has failed to reach ; the land in the distance is the island of Ovalau, only twelve miles away, where a series of severe outbreaks have occurred.

B. Spraying tall coconut trees at Carvaci on Ovalau, xi/25, with a Fitz-Henry Guptill solid stream type of spraying machine.

C. Spraying taller trees, 60–80 ft., with the same machine on Yanuthalailai, xi/25. In both cases the material used was arsenate of lead suspended in sea-water.

PLATE XIII

PLATE XIV

A

B

C

PLATE XIV

CAGES AND THE INSECTARY

A. Landing the first colony of *Ptychomyia* to be liberated away from Suva. Caboni Province of Ra, ix/25.

B. The insectary at Suva in which secondary parasites on *Ptychomyia* were killed off. The screen used has sixty-five meshes to the lineal inch. There are double doors, and isolation from ants, etc., is secured by the supporting posts being set in cups of water.

C. Some of the *Ptychomyia* breeding cages in a shelter just outside the insectary. Note the young coconut palms or " varas " planted in benzine tins.

PLATE XV

METHOD OF COLONISING *PTYCHOMYIA*

A. A colony of 700 *P. remota* liberated on the island of Naigani, xi/25. About eighty parasitised larvae are feeding upon each young coconut or " vara." The tins are insulated by tanglefoot bands round the supports.

B. A colony of *P. remota* ready for liberation.

C. A " vara " on which parasitised *Levuana* larvae have been depastured. Note the defoliated appearance of the leaves and the small white cocoons. A small strip of fibre is tied on the leaf-stalk to provide additional space for the larvae to pupate. This cage is one of the seventeen that came from the F.M.S.

PLATE XV

A

B

C

PLATE XVI

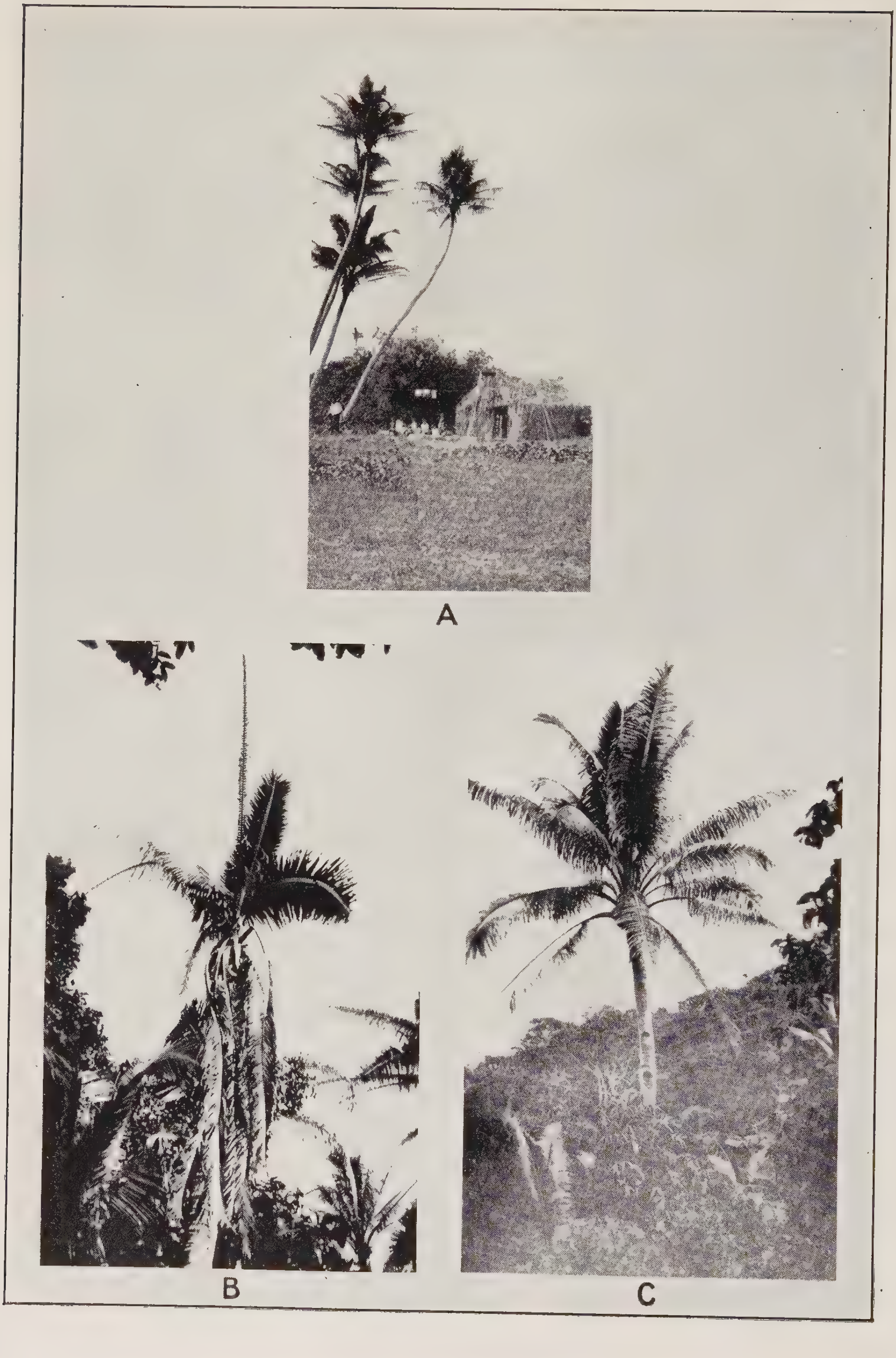

PLATE XVI

TYPICAL INJURY CAUSED BY *LEVUANA*

A. Trees just recovering from a severe outbreak. The top four or five leaves are green and much under-sized; the lower leaves have been eaten away, and are useless. Naigani island, iv/25, taken three months after an outbreak cleared up from food shortage.

B. Tree showing the effects of a very severe attack. Its recovery is doubtful because it has been able to put out only one and one-half green leaves in the past three months in lieu of the normal three. Note the vertically projecting leaf which is skeletonised except for the basal part of each leaflet. Naigani, iv/25.

C. An extensively defoliated tree. Note the gradual whitening of the lower leaves. Lovoni, Ovalau, iv/26.

PLATE XVII

THE EFFECT OF LIBERATING *PTYCHOMYIA*

A. The island of Toberua on which *Levuana* became very abundant on the leeward side (facing the camera). The increase in the percentage parasitism of *P. remota* during three successive broods of the moth was very rapid.

B. A tree (to the left of centre) on the island of Yanuthalailai with *Levuana* scars on the middle tier of leaves only. The moth was beginning to "flare up" on this island when *P. remota* brought it under control. The attack on this tree had cleaned up when the photo was taken. When a moth flight takes place, the eggs are laid first on the upper leaves (those now middle-aged were newly opened when the tree became infected), and the lower leaves are then progressively attacked if nothing interferes with the progress of the moth.

C. An early colony of *P. remota* liberated at Nuibasaga, Moturiki, xi/25.

PLATE XVII

A

B

C

PLATE XVIII

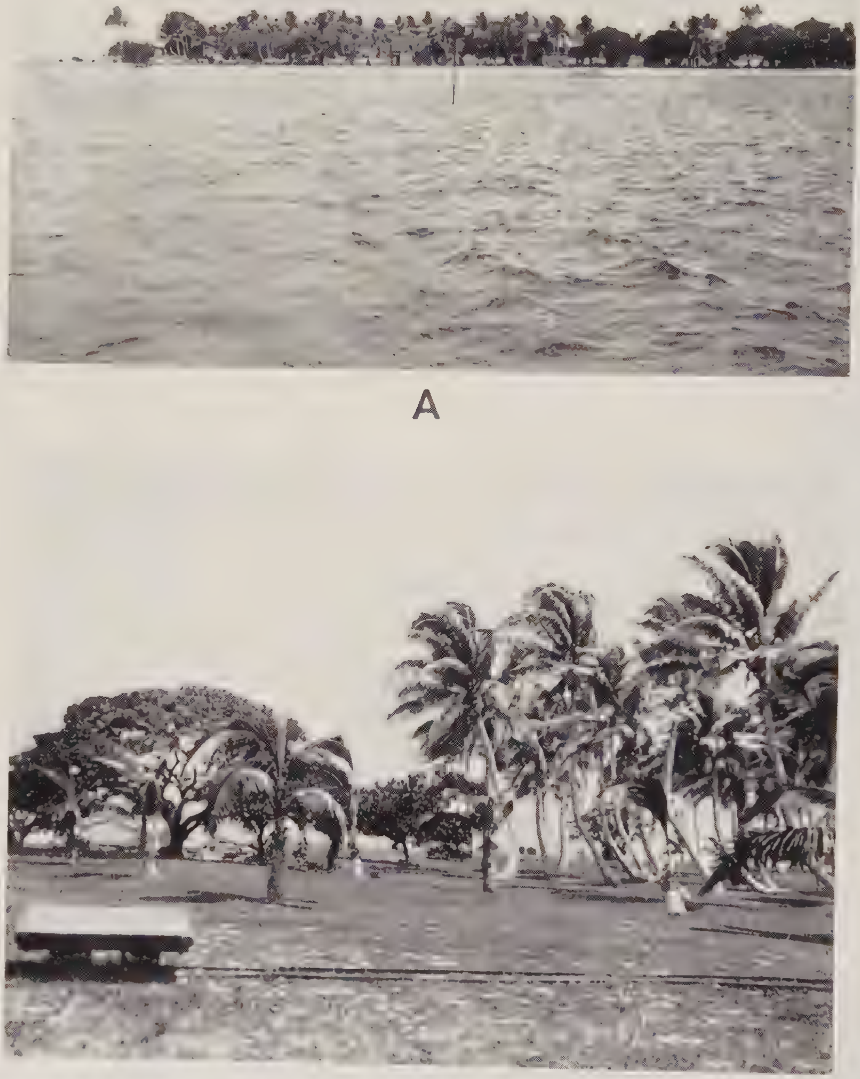

PLATE XVIII

Conditions on Makuluva

A. The leeward side of this little island showing the belt of infested trees.

B. Trees on the leeward side of Makuluva. *P. remota* now prevents *Levuana* clearing up from food shortage, and as there are no secondary hosts the fly is unable, without overlapping broods of the host, to bring about a high enough parasitism to enable predators to complete the work of extermination. *Levuana* therefore continues to exist, and was observed on this island in November 1928 after three years of *P. remota*. Photo taken in xii/1927.

PLATE XIX

Conditions on Makuluva

A. Small tree on lee side of the island completely defoliated in December 1927.

B. Five-year old trees on lee side of the island stunted by repeated *Levuana* attacks. Photo taken in December 1927.

PLATE XIX

A

B

A

B

PLATE XX

Conditions on Makuluva

A. A typical example of the effect of repeated attacks of *Levuana.* Note the tapering trunk that has many small constrictions each dating from an attack ; the lack of foliage and finally the short and newest leaves that give to the tree a flat-topped appearance.

B. Leaves of one tree laid out in order of age, the youngest being nearest to the camera. This was the standard method of examining trees felled for purposes of detailed examination of *Levuana* injury.

PLATE XXI

A. When bananas grow amongst coconuts that are heavily infested with *Levuana* the eggs and larvae of the moth can sometimes be found on the banana leaves. They were present on the bananas shown in this photo taken at Nanuku in June 1925.

B. A tree completely defoliated by *Levuana* but which had been free from the pest for several years prior to 1926, this being shown by the absence of trunk constrictions and by the presence of nuts. Navini, Yasawa Group, October 1926.

C. Leaf of Niu Sawa, *Veitchia joannis*, showing maximum *Levuana* defoliation. Only the extreme basal portion of each leaflet is eaten. Our assistant Jacobi holds the leaf. Ovalau, March 1926.

PLATE XXI

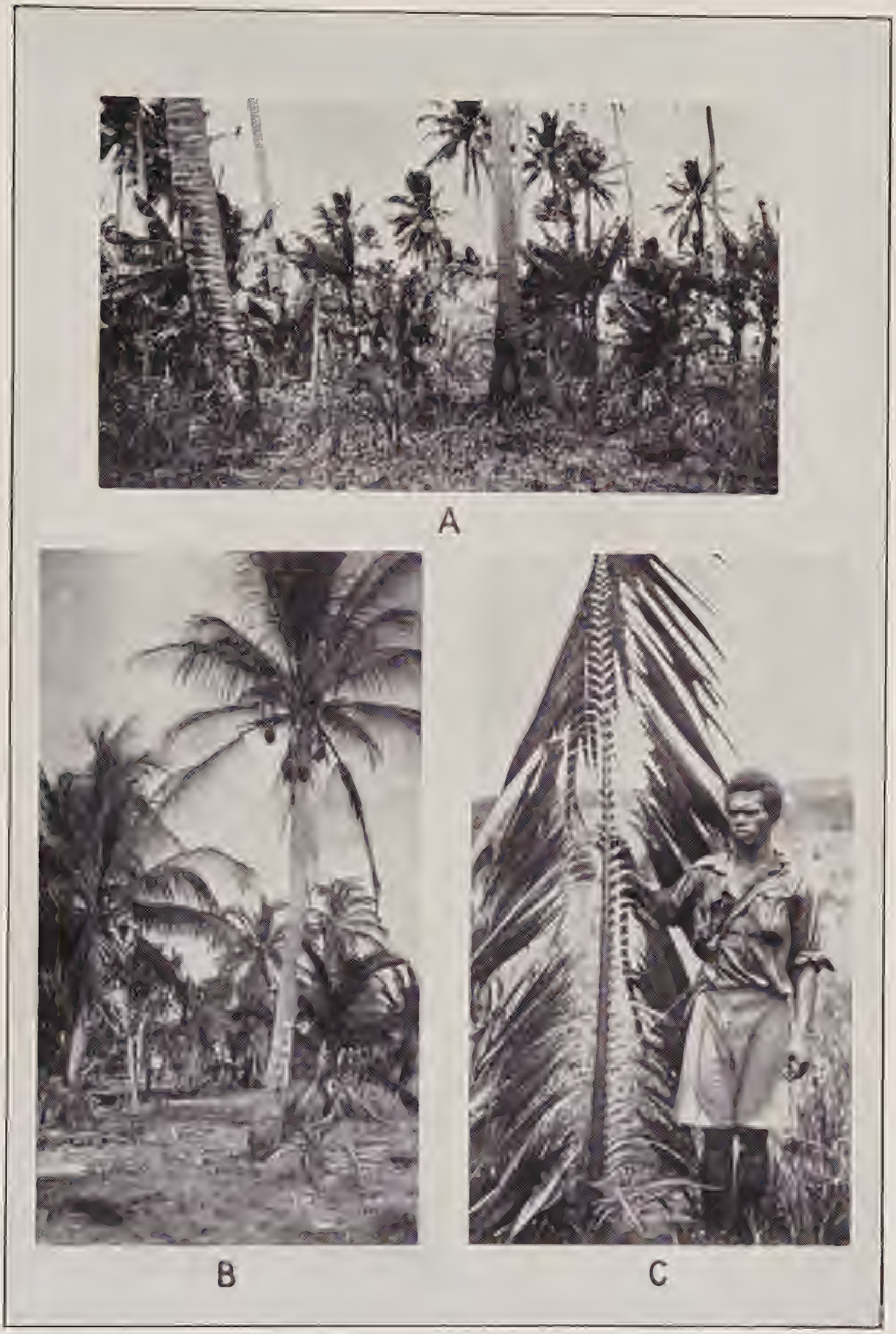

PLATE XXII

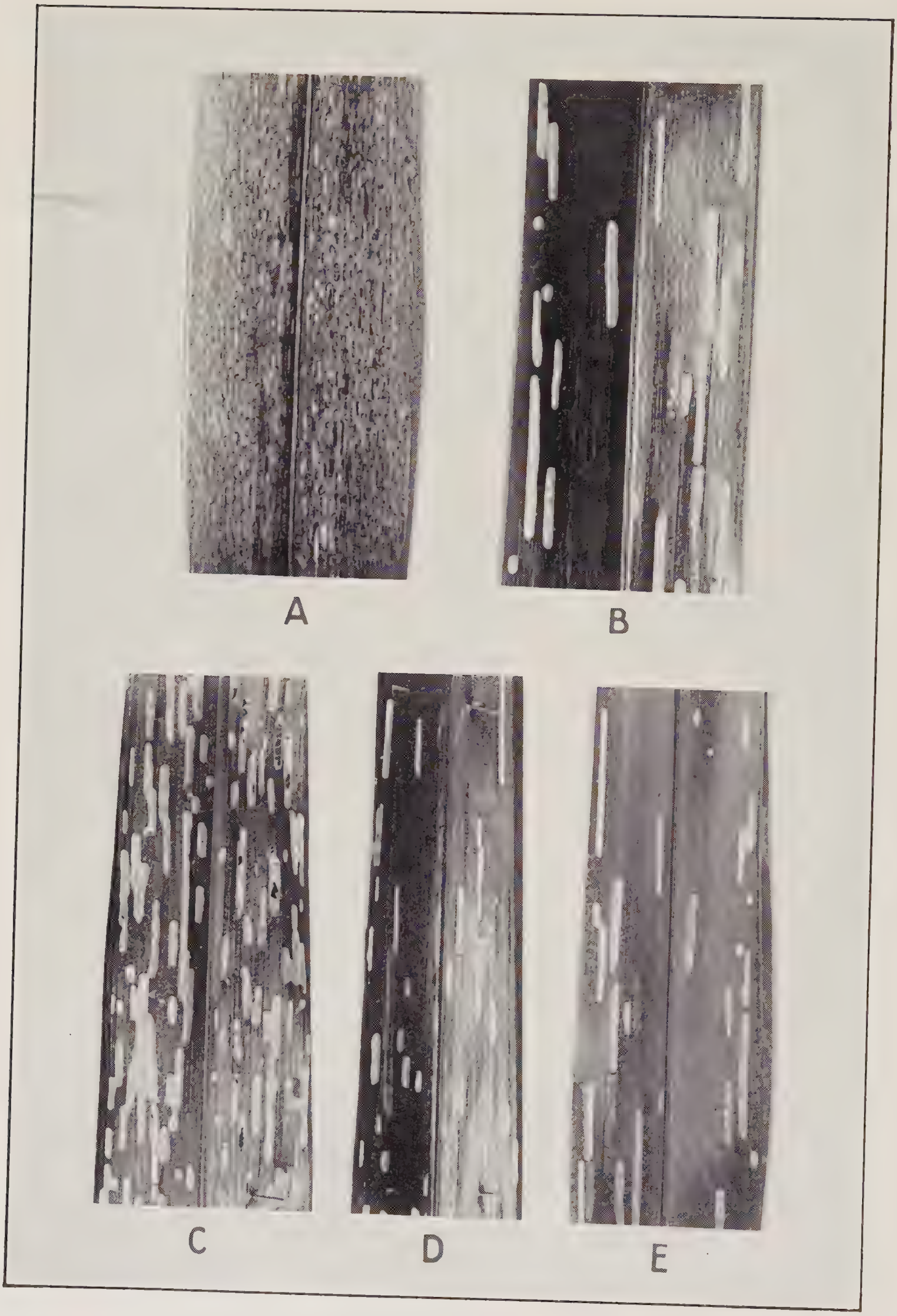

PLATE XXII

FEEDING SCARS OF *LEVUANA*

A. Under surface of leaf with almost complete defoliation by scars made by first, second, and third stage larvae.

B. Scars made by fourth and fifth stage larvae.

C. Old feeding scars made by large larvae. Photo taken from the upper surface of the leaf. Note that some of the upper epidermis and cuticle of the leaf has fallen out.

D. Old and new scars. View of upper surface.

E. Old and new scars. View of under surface.

PLATE XXIII

A. Heavily defoliated leaf with abnormally large percentage of small scars.

B. Upper surface of E—see E for description.

C. Lower surface of leaf heavily defoliated by small scars.

D. Lower surface of F. The feeding scars have been made by larvae of the brown moth, *Agonoxena argaula.*

E. Lower surface of B. Newly-formed scars are dark, the older ones from which powdered " sear tissue " has fallen being lighter in colour.

F. Upper surface of D. Typical *A. argaula* feeding scars.

PLATE XXIII

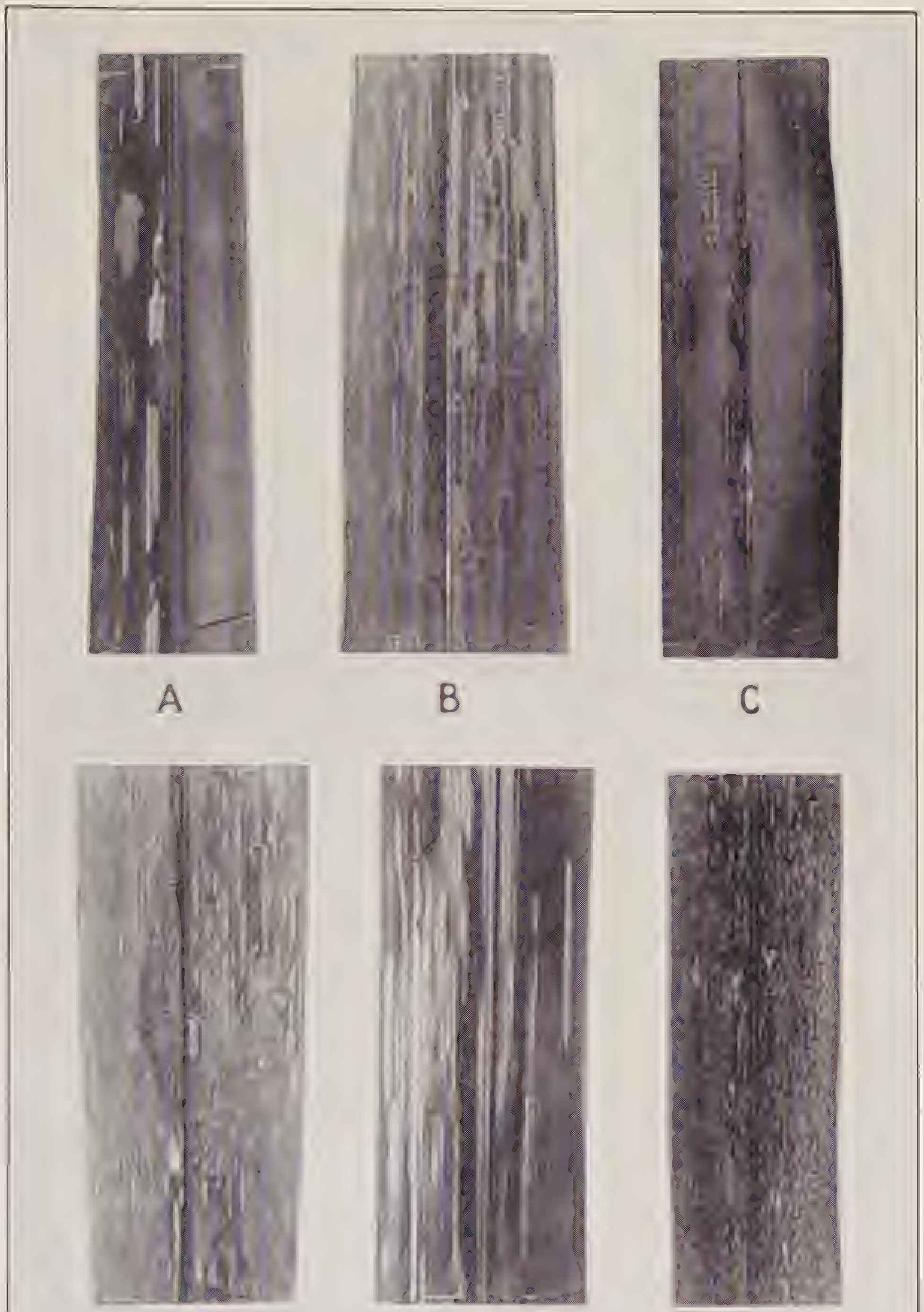

PLATE XXIV

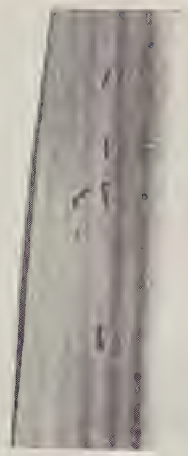

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PLATE XXIV

LEVUANA LIFE-HISTORY—EGGS AND YOUNG LARVAE

A. Third-stage larvae feeding on a coconut leaf, $\frac{5}{6}$ natural size. The large feeding scar above and slightly to the left of centre is made by *A. argaula*, the " brown moth."

B. First-stage larvae just hatched feeding on the egg-shells, $\frac{5}{6}$ natural size.

C. Egg clusters of *Levuana*, $\frac{5}{6}$ natural size. Note the variation in form of cluster.

PLATE XXV

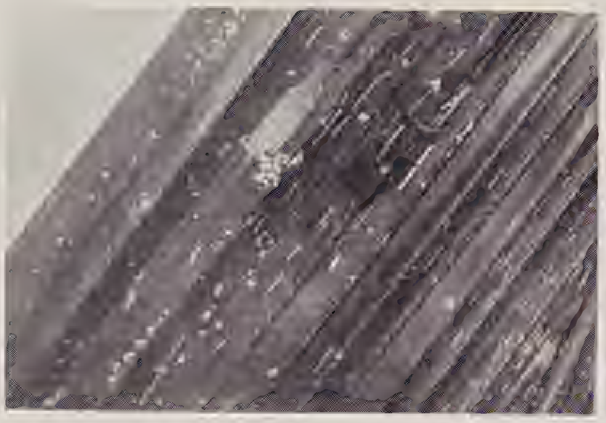
Levuana Life-history—Larvae

A. Third-stage larvae, $\frac{5}{6}$ natural size.

B. Ditto.

C. Third-stage larvae contracted for the third moult, $\frac{5}{6}$ natural size.

PLATE XXV



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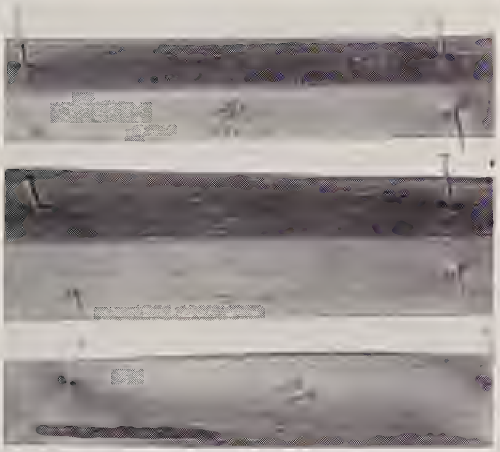

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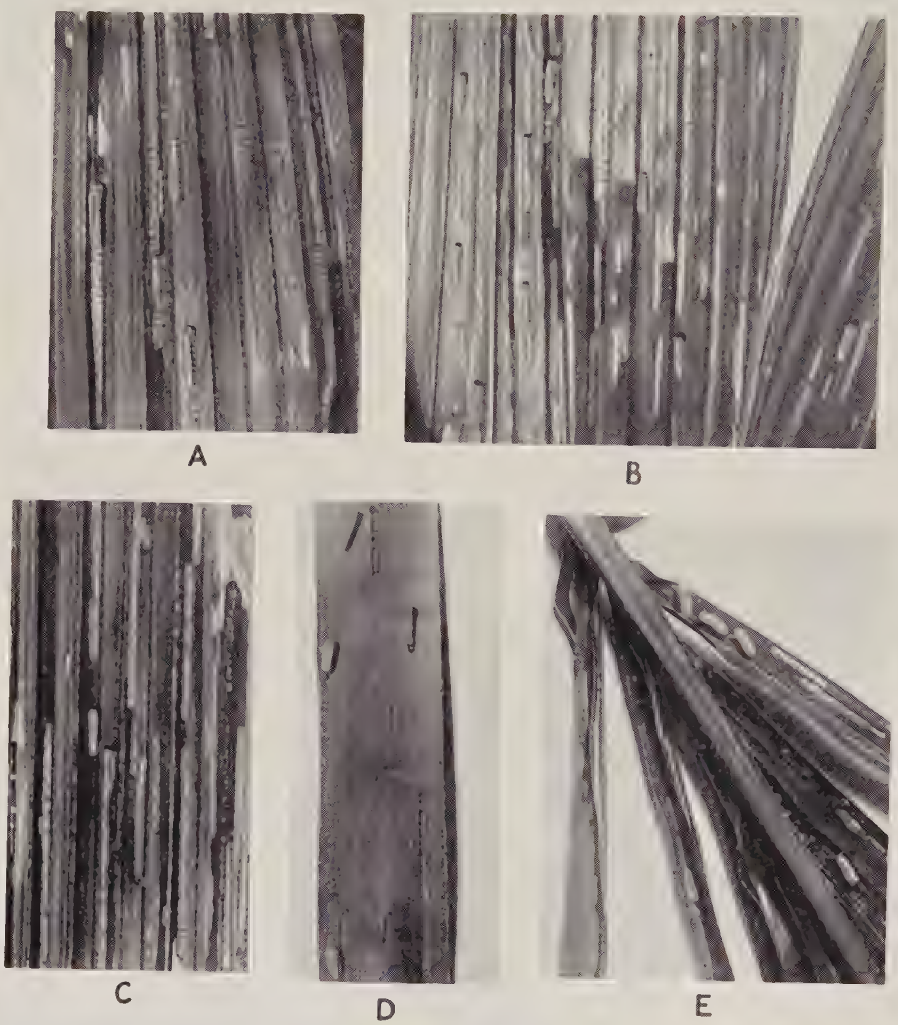
PLATE XXVI



A

B

C

D

E

PLATE XXVI

LEVUANA LIFE-HISTORY—LARVAE

A. Fifth-stage larvae feeding, $\frac{5}{6}$ natural size.

B. Fourth-stage larvae feeding, $\frac{5}{6}$ natural size.

C. Ditto.

D. Third-stage larvae feeding, $\frac{5}{6}$ natural size.

E. Larvae preparing to moult in the typical situation at the base of the leaflets. Note the old moult skins, $\frac{5}{6}$ natural size.

PLATE XXVII

LIFE-HISTORY OF *LEVUANA*—PUPAE AND PREPUPAE

A. A mass of freshly formed cocoons in a typical situation on inner side of leaf stalk base, $\frac{1}{2}$ natural size.

B. Prepupae arranged in an age series with the youngest at the left, $\frac{5}{6}$ natural size.

C. On left three pupae followed by four stages in development of pupa; the left one in each pair being venter uppermost, $\frac{5}{6}$ natural size.

D. Six pupae in top row showing range in size; seven prepupae in lower row newly formed on left, ready to pupate on right, $\frac{5}{6}$ natural size.

PLATE XXVII

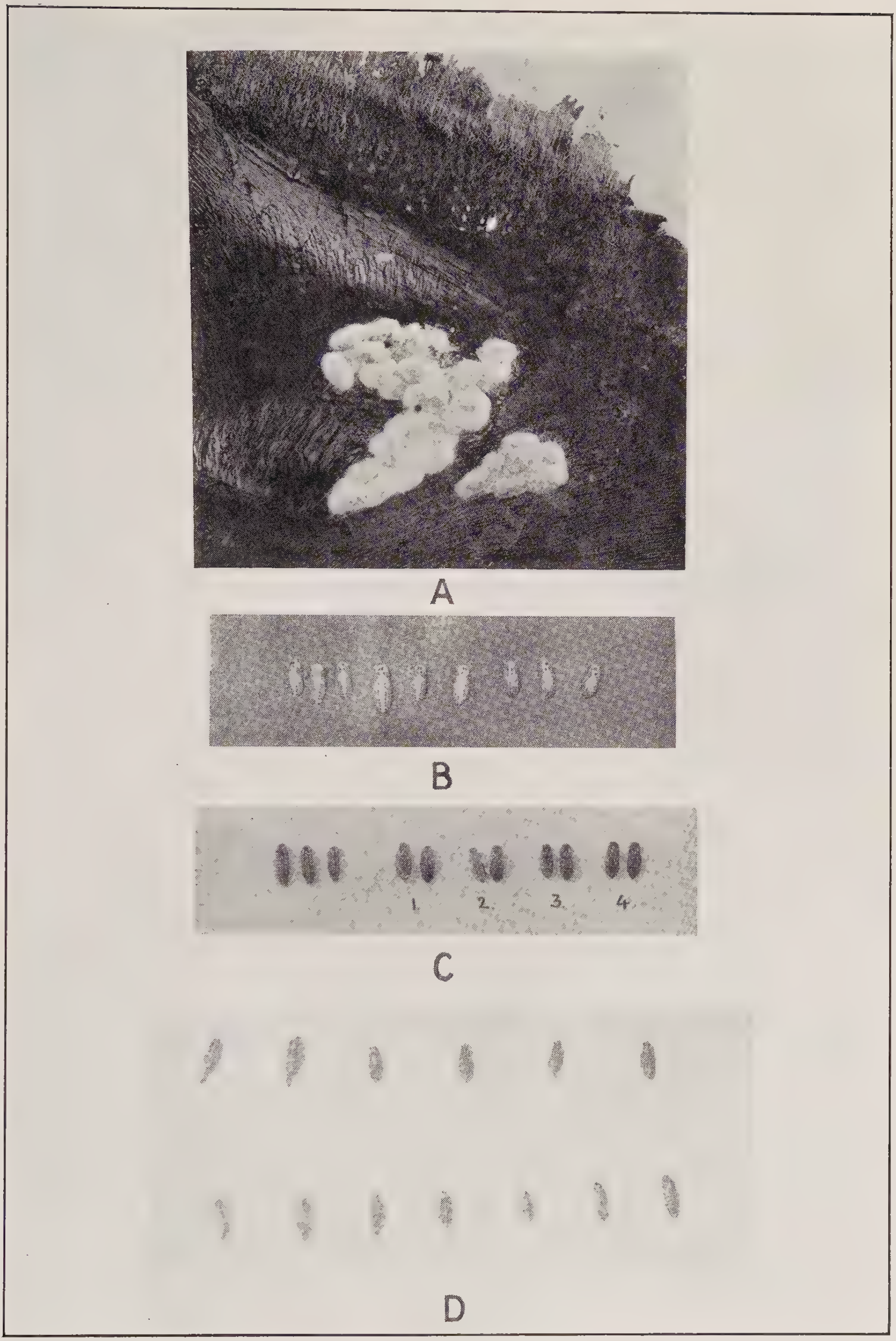


PLATE XXVIII

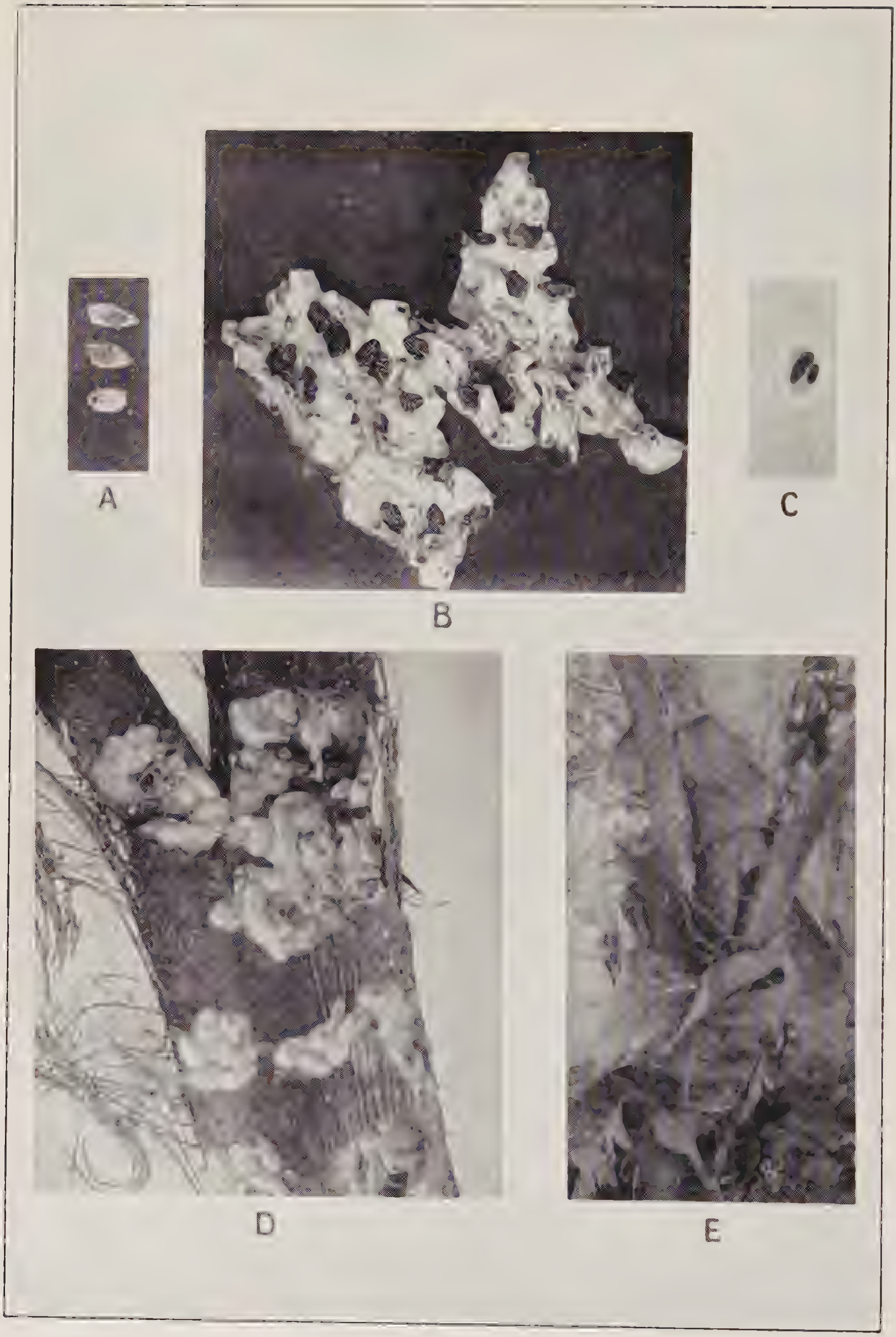


PLATE XXVIII

COCOONS

A. Cocoons of *Levuana* parasitised by *P. remota.* The top one shows a dead *Levuana* larva with a *P. remota* cocoon lying alongside ; centre, a fly puparium beneath cocoon (turned over like the top one with a needle) ; the lower one shows a fly emergence hole.

B. Mortality of moths due to overcrowding. This is the underside of a mass of old cocoons showing numerous dead mature pupae with characteristic distortion due to pushing through overlying cocoons, $\frac{5}{6}$ natural size.

C. A cocoon turned over to show the fly puparium at right and the dead host carcase at left, $\frac{5}{6}$ natural size.

D. Old cocoons on base of leaf. Some projecting pupal skins can be seen, also some fly puparia, $\frac{1}{3}$ natural size.

E. *Levuana* cocoons *in situ* on leaf bases and on the " vulu " or matting connecting the leaf bases.

PLATE XXIX

ADULTS OF *LEVUANA*

A. ♂ on right and ♀, $\frac{5}{6}$ natural size.

B. ♂ on right and ♀, $\frac{5}{6}$ natural size.

C. ♂ and ♀ *in copula*, $\frac{5}{6}$ natural size.

D. ♂ in tube and ♀, $\frac{5}{6}$ natural size.

PLATE XXIX

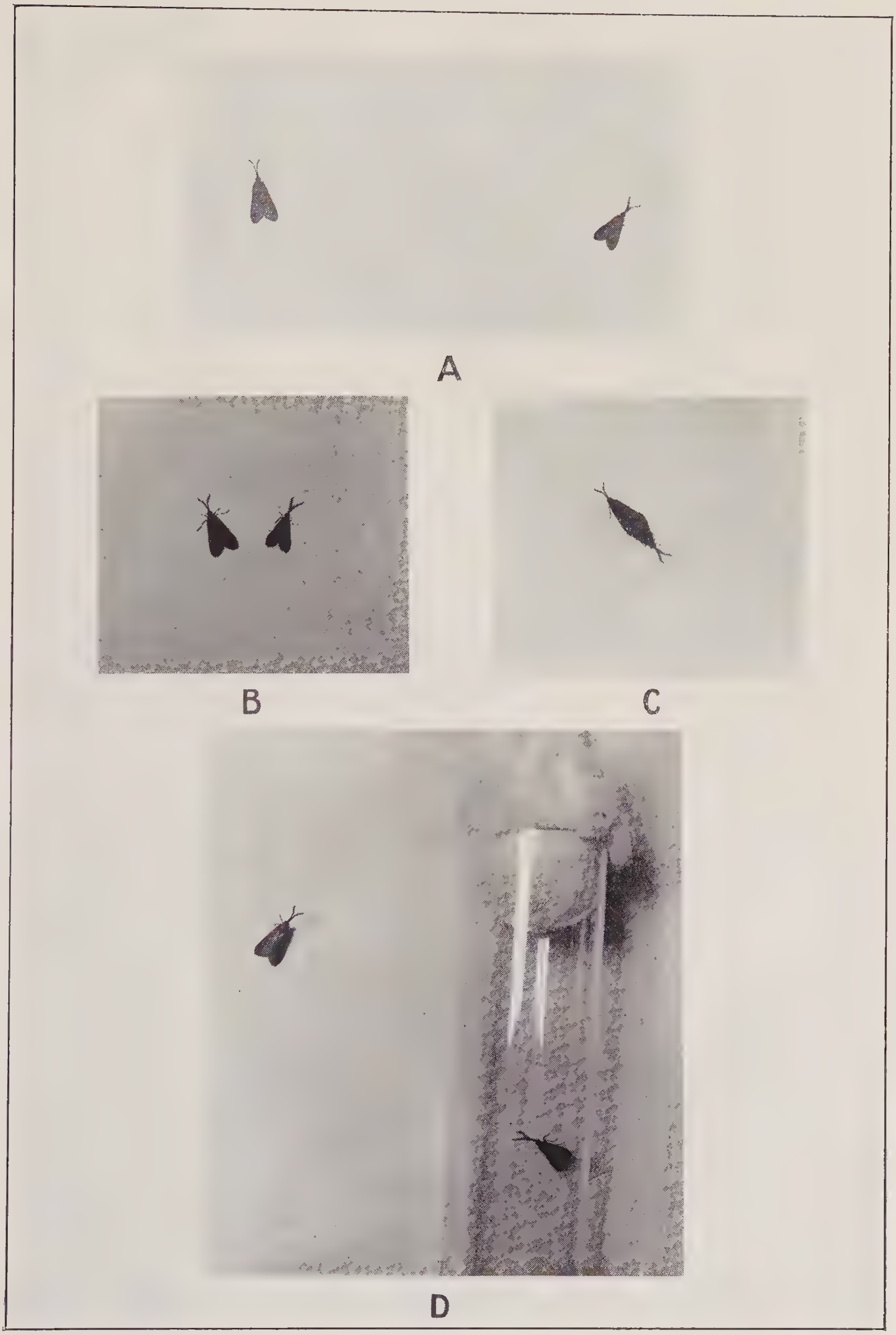


PLATE XXX

STAGES OF *LEVUANA IRIDESCENS*, B. B.

FIG. 1.—*L. iridescens*, adult ♂ in resting attitude. × 7.

FIG. 2.—*L. iridescens*, adult ♀ in resting attitude. × 7.

FIG. 3.—Egg-cluster of *L. iridescens* on coconut leaf. These eggs are more than two days old and show the red pigment which is absent in newly laid eggs. × 2·7.

FIG. 4.—Fifth instar larva of *L. iridescens*. × 8·9.

FIG. 5.—Pupa of *L. iridescens*. × 8·2.

PLATE XXX

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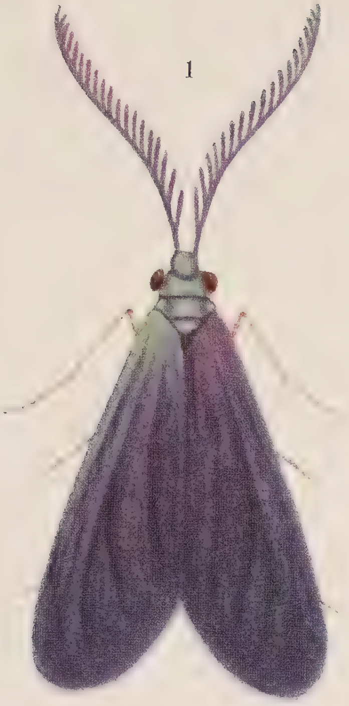

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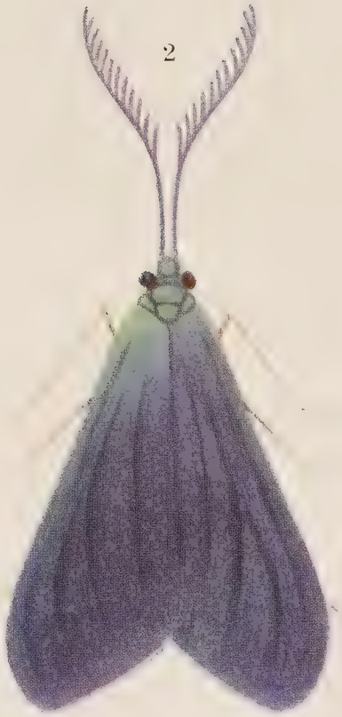

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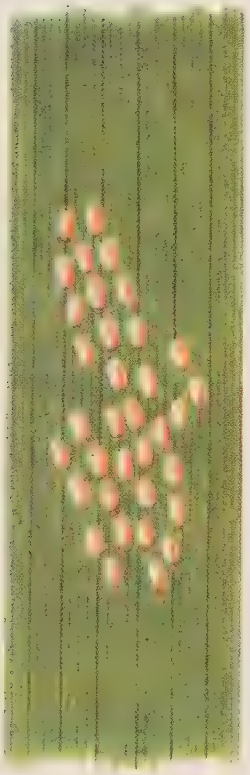

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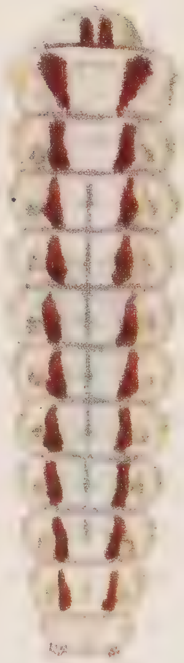

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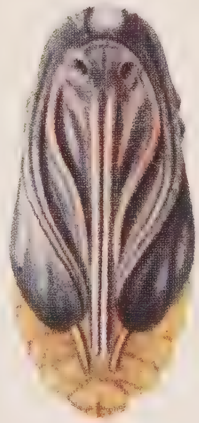

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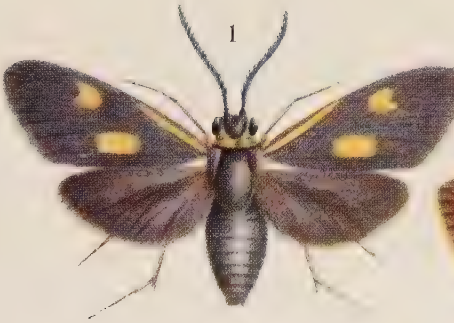
PLATE XXXI

ALLIED ZYGAENID MOTHS

FIG. 1.—*Artona A. trisignata*, Snell. × 4·5.
FIG. 2.—*Artona catoxantha*, Hmps., ♂. × 4·5.
FIG. 3.—*Levuana iridescens*, B. B., ♀. × 4·5.
FIG. 4.—*Artona albicilia*, Hmps. × 4·5.
FIG. 5.—*Heteropan dolens*, Druce. × 3·6.
FIG. 6.—Zygaenid F. × 4·5.

PLATE XXXI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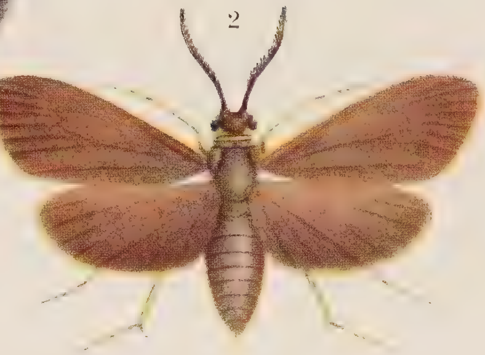
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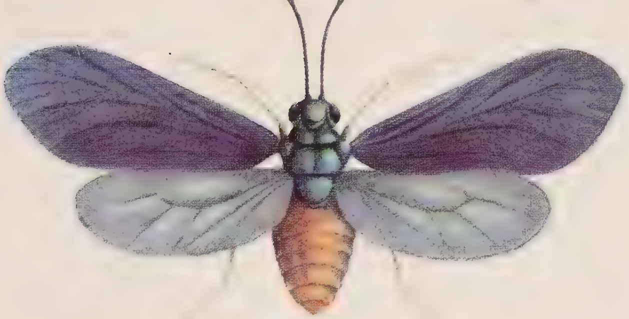
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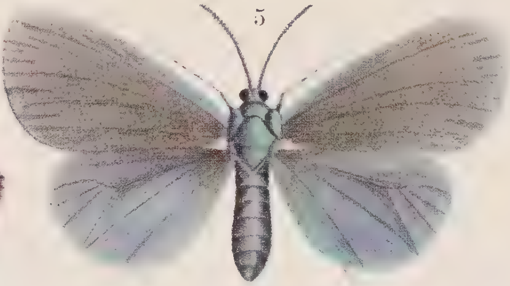
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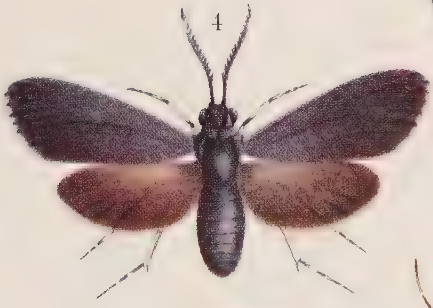
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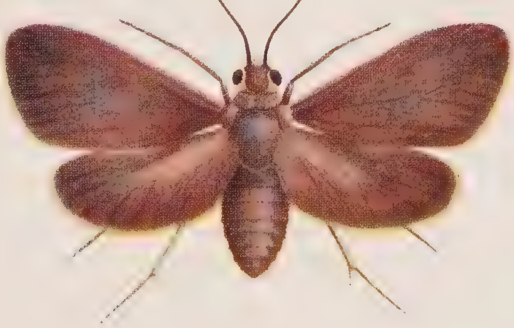
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PLATE XXXII

NATURAL ENEMIES OF *ARTONA* INTRODUCED INTO FIJI

FIG. 1.—Adult *Ptychomyia remota,* Aldr. × 11·8.

FIG. 2.—Cocoon of *Levuana iridescens*, B. B., showing skin of larva and pupa of *P. remota*. × 5·9.

FIG. 3.—Side view of head of *P. remota*. × 56.

FIG. 4.—Larval skin of *L. iridescens* after *P. remota* has left it. × 6·7.

FIG. 5.—*Callimerus arcufer*, Chap., adult. × 5.

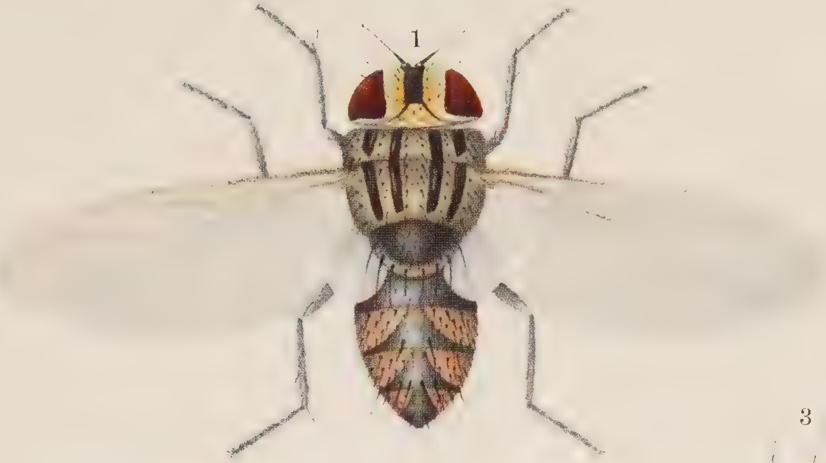
FIG. 6.—*C. arcufer*, larva. × 8·4.

FIG. 7.—*C. arcufer*, head of ♂. × 6·6.

FIG. 8.—*C. arcufer*, head of ♀. × 6·6.

PLATE XXXII

1



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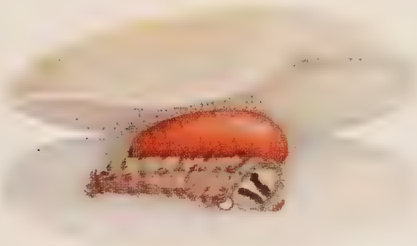

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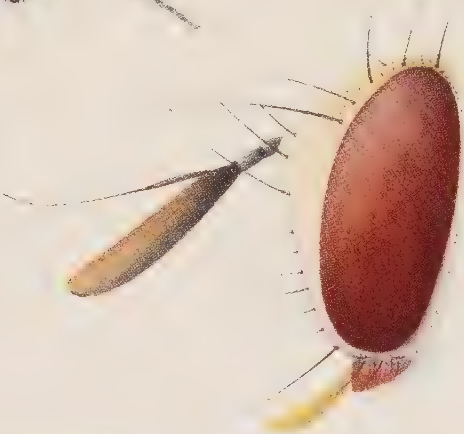

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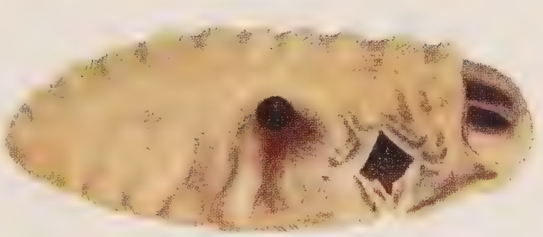

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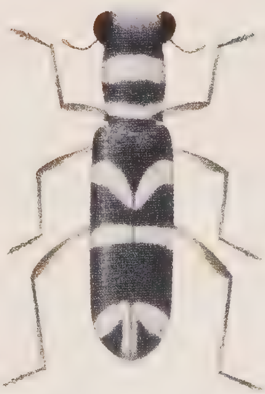

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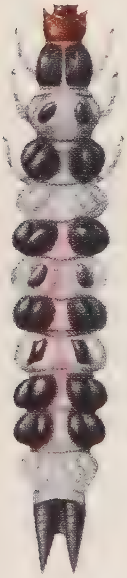

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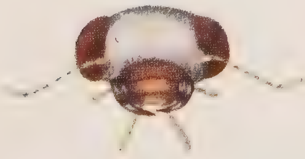

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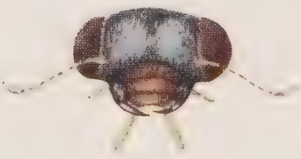

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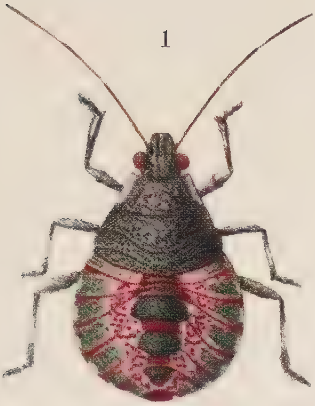
PLATE XXXIII

Predatory Bugs present in Fiji

Fig. 1.—*Cantheconidea cyanacantha*, Stål, third-stage nymph. × 9.
Fig. 2.—*C. cyanacantha*, adult. × 4·5.
Fig. 3.—*Platynopus melanacanthus*, Boisd., third-stage nymph. × 9.
Fig. 4.—*P. melanacanthus*, adult. × 4·5.
Fig. 5.—*Oechalia consocialis*, Boisd., fourth-stage nymph. × 9.
Fig. 6.—*O. consocialis*, adult. × 4·5.

PLATE XXXIII

1



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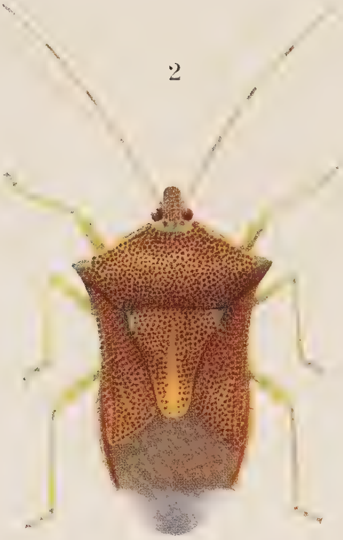

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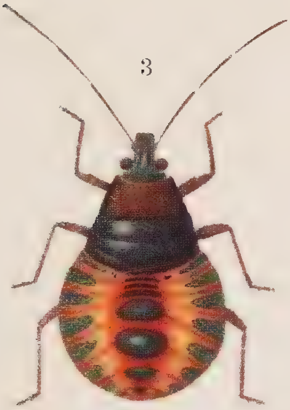

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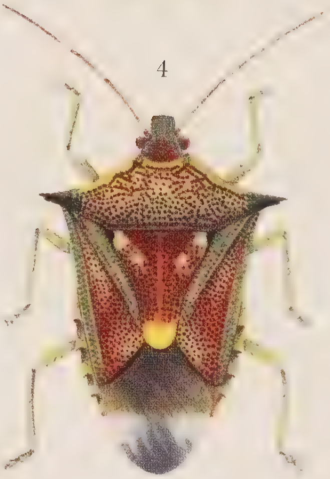

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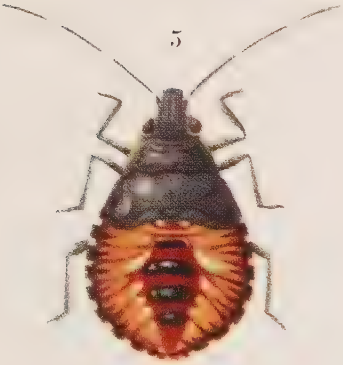

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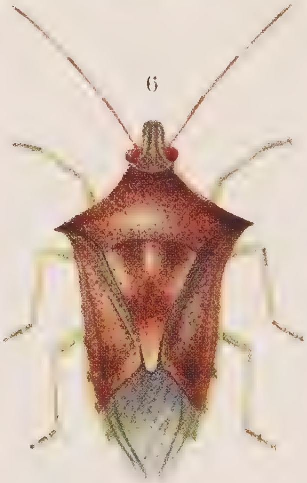

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PLATE XXXIV

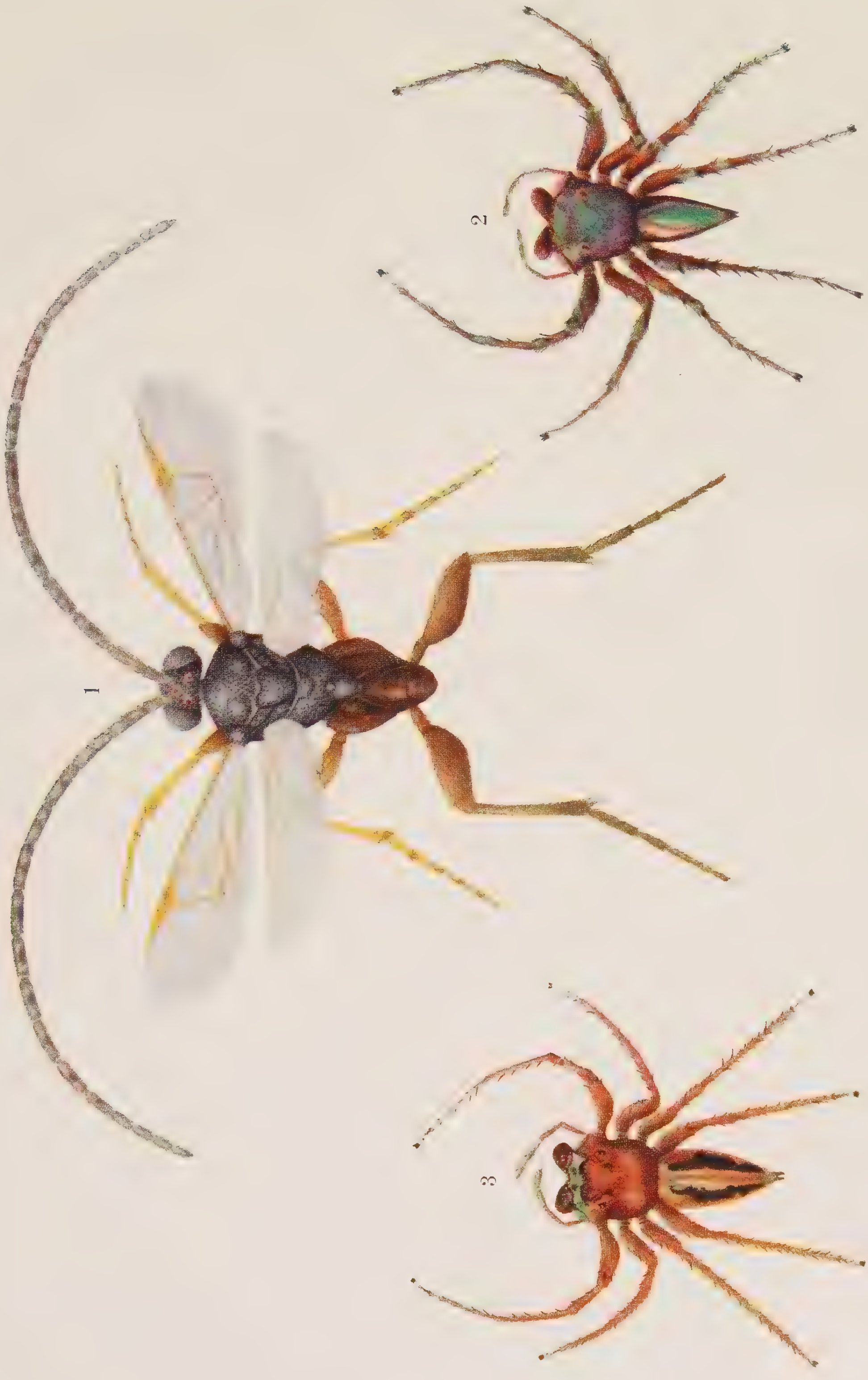
MISCELLANEOUS ENEMIES OF ZYGAENIDS

FIG. 1.—*Apanteles artonae*, Rohw., parasitic on *Artona catoxantha*, Hmps., in Malaya. ♂ × 11·4.

FIG. 2.—An Attid spider, *Ascyltus pterygodes*, Koch, predacious on *Levuana iridescens*, B. B., in Fiji. ♂ × 3·2.

FIG. 3.—*A. pterygodes*, ♀. × 3·2.

PLATE XXXIV



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